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ACTINOSPHAERIUM EICHORNI.

A BIOMETRICAL STUDY IN THE MASS RELATIONS OF NUCLEUS AND CYTOPLASM*.

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Introduction.

THE following study is concerned with what appears at present to be the critical problem of cytology, the inter-relation of nucleus and cytoplasm, or more strictly of chromatin and cytoplasm. Much knowledge of chemico-physiological significance is possessed by naturalists on this head, but concerning the mass relations that hold between chromatin and cytoplasm under different physiological conditions, a knowledge of which one would consider fundamental from a chemico-physiological point of view, strangely little is known. How important this mass relation may be is brought home to one who remembers that the most obvious distinction between the male and female sexual cells throughout organic nature is this very one of the mass relations between chromatin and cytoplasm.

In order that the following observations and experiments on *Actinosphaerium* may be easily grasped, I will shortly recapitulate the history of its encystment and reproduction.

Encystment may be induced by starvation for a longer or shorter period. The creature about to encyst becomes much vacuolated, and fixes itself to the vessel in which it is confined, withdrawing its pseudopodia. The endoplasm becomes exceedingly opaque, appearing conspicuously white to the naked eye, and shortly afterwards it breaks up into a varying number of discoid bodies lying in the gelatinous exoplasm, each of which contains a single nucleus. During the course of the next twenty-four hours each mother cyst divides to form two daughter cysts; the nucleus of each daughter cyst now divides twice, giving off

* By the permission of the authorities of New College, Oxford, I was enabled to work in Professor R. Hertwig's laboratory at Munich during part of the winter of 1902. Through his attention and guidance it has been possible to bring this research to some result.

two polar bodies; the daughter cysts then fuse, about twenty-four hours after their formation, sister with sister, to form circular discoid conjugation cysts each containing a conjugation nucleus. The conjugation cysts form thick siliceous coats and remain in this condition for several weeks.

Preliminary Experiments and Observations.

The free living *Actinosphaeria* possess a great many more nuclei than the few that are preserved for this process of encystment: my first object therefore was to determine roughly how many nuclei are thrown away in the process of encystment. For this purpose I took several hundred individuals of various sizes, measured them*, put three-quarters to starve and in consequence to encyst (at room temperature 15°—19° C.), and killed and stained the remaining quarter in order to count their nuclei. The results of these two experiments are set forth in Tables I. and II.

TABLE I.

Diameter of Individuals in Micrometer Units.

Number of cysts built at 15°—19° C.	*15*	*17*	*19*	*21*	*23*	*25*	*27*	*29*	*31*	Totals
1	1	—	—	—	—	—	—	—	—	1
2	2	3	—	—	—	—	—	—	—	5
3	—	4	3	4	2	—	—	—	—	13
4	—	—	2	3	5	1	1	—	—	12
5	—	—	—	4	3	2	1	1	2	13
6	—	—	—	4	5	1	1	2	—	13
7	—	—	—	1	3	5	—	7	—	16
8	—	—	—	—	1	1	3	3	1	9
9	—	—	—	—	2	—	3	4	—	9
10	—	—	—	—	2	—	—	1	4	7
11	—	—	—	—	—	—	1	1	1	3
12	—	—	—	—	—	—	—	2	3	5
13	—	—	—	—	—	—	—	—	1	1
14	—	—	—	—	—	—	—	—	1	1
15	—	—	—	—	—	—	—	—	1	1
Totals	3	7	5	16	23	10	10	21	14	109

* Every precaution was taken to ensure accuracy in the measurement. Each specimen was measured with a micrometer under Zeiss AA, 2, the unit of measurement being one division of an eye-piece micrometer, which was found with the objective used to correspond to 1·81 μ. The creatures were selected for measurement only when the pseudopodia were fully expanded, the contour of the body was circular, and the creature was suspended freely in a drop of water. The diameter of the body was then taken from edge to edge, ignoring the pseudopodia. The difficulty of determining the correlation between the size of *Actinosphaeria* and the number of cysts built was encountered chiefly in the liability of the creatures to divide or fuse one with another (plastogamy) after they had been placed in the vessels to starve and to encyst. To avoid mistakes from this cause the vessels were kept as constantly under supervision as possible, and discretion has been used in various ways: but absolute accuracy in cases of such difficulty can hardly be ensured.

TABLE II.

Diameter of Individuals in Micrometer Units (unit of measurement = 1·81 μ).

Number of Nuclei.	19	21	23	25	27	29	31	Totals
50	1	—	—	—	—	—	—	1
100	3	4	—	—	—	—	—	7
150	2	8	11	—	1	—	—	22
200	—	3	7	8	2	—	—	20
250	—	—	1	10	4	1	—	16
300	—	—	—	1	7	2	—	10
350	—	—	—	—	—	2	1	3
400	—	—	—	—	—	3	3	6
450	—	—	—	—	—	2	1	3
500	—	—	—	—	—	3	1	4
550	—	—	—	—	—	1	—	1
600	—	—	—	—	—	1	1	2
650	—	—	—	—	—	—	1	1
Totals	6	15	19	19	14	15	8	96

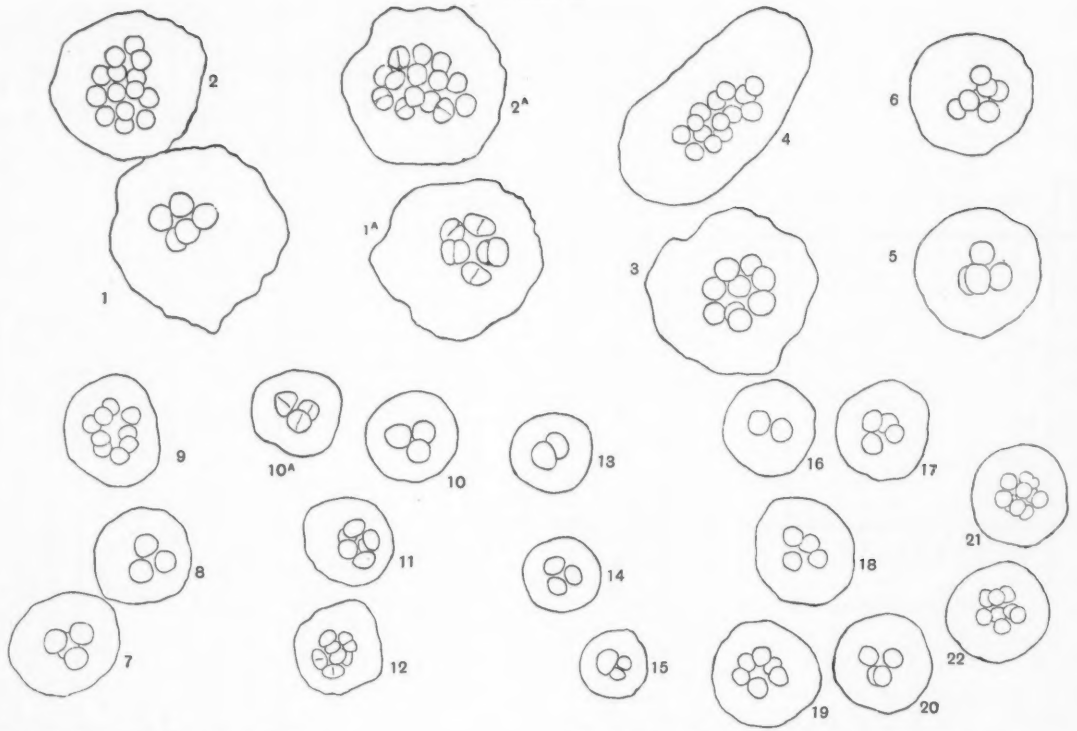
Table I. records the correlation between size of *Actinosphaerium* and the number of cysts built. The correlation coefficient = 0·7692 ± ·0264. The standard deviation of the sizes is 4·4372 units = 8·031 μ; that of the numbers of cysts is 2·9478.

Table II. records the correlation between size of *Actinosphaerium* with number of nuclei. Correlation coefficient = ·8540 ± ·0168. The standard deviation of the sizes is 3·4094 units = 6·171 μ, that of the numbers of nuclei is 2·5181 × 50. The two correlation coefficients here obtained are exceedingly high, as high as those we find between corresponding bones of two fingers of the same hand, etc. It would be interesting to see whether equally high coefficients obtain for multinucleate *Protozoa* in general.

The above correlation tables had shown that great variability existed in *Actinosphaeria* of similar bulk as to the number of nuclei they contained and as to the number of cysts they built during encystment, and that these two variables corresponded in a certain degree. In the course of counting and observing the cysts tabulated in Fig. B. I became gradually impressed with a further fact, namely, that the cysts built by different individuals were often of very different sizes, and moreover that the size of the cyst seemed to bear a certain relation to their number: i.e. when an *Actinosphaerium* had built very numerous cysts for its size then those cysts were generally small, and *vice versâ*. On Plate I. Figs. 1A—15 are collected the most striking examples of this fact, which I could gather from these first experiments. Here it will be seen that in *Actinosphaeria* of all kinds of sizes individuals occurred, some of which built numerous and small cysts, while others built fewer and larger.

The next preliminary experiments were directed towards finding out what effect would be produced on the number and size of the cysts by subjecting the animals to different temperatures. Animals of a certain size (36·2—39·8 μ) were selected: half were placed in an incubator at 24°—26° C., the other half were placed in an unheated room where the temperature varied between 7° and 12° C.

PLATE I.



Figs. 1A, 2A. Two individuals forming daughter cysts.
Figs. 1, 2. Same as above, having formed conjugation cysts.
Figs. 3, 4, 5, 6, 7, 8, 9, 10, 11. Individuals of various sizes in conjugation cyst stage.
Fig. 10A. Daughter cysts not yet fused.

Figs. 12, 13, 14, 15. Mother and daughter cysts.
Figs. 16, 17, 18, 19, 20. Individuals with conjugation cysts made at 24°—26° C.
Figs. 21, 22. Conjugation cysts at 7°—12° C.
All figures drawn to scale under Zeiss AA, 2.

In 60 hours the individuals of the warm culture were already in the conjugation-cyst stage, while the similar cold culture was not in a similar stage of encystment till a week and four days after it was prepared. The two cultures built cysts in the following numbers:—

No. of cysts	2	3	4	5	6	7	8	9
Frequency in warm culture	2	4	6	1	3	0	0	0
Frequency in cold culture	0	0	1	1	2	1	3	2

The reason why fewer reached the conjugation cyst stage in the cold culture was that owing to the delayed encystment the culture had to be more frequently weeded of individuals that had divided etc. This experiment suggested that the higher temperature caused fewer cysts, and the cold caused more numerous cysts to be built, while on Plate I. Figs. 16—22 show that the rule adumbrated by the previous experiment is confirmed by these, since the cysts formed in the cold being more numerous are at the same time smaller than the comparatively few cysts built in the warm.

The preliminary experiments now described had suggested the following facts and problems:

A. An *Actinosphaerium* of a given size may contain a number of nuclei varying between wide extremes and in consequence—

B. It may build a varying number of cysts.

C. When it builds few cysts for its size then the cysts tend to be large; when it builds many they tend to be small.

D. An increased temperature hastens on encystment, a low temperature retards it.

E. An increased temperature causes fewer and larger cysts to be built, a low temperature causes many and smaller, i.e. an increased temperature causes a greater percentage of nuclei to be thrown away.

F. In what way does the temperature act upon the number of nuclei rejected? That is, does the temperature affect the number of nuclei gradually, or only at the period when they are being rejected?

G. In what way does the size of the cyst affect the nucleus contained? That is, does the nucleus vary in correspondence to the varying size of the cyst or does it remain the same so that a different mass-relation between nucleus and cytoplasm occurs in the different cases?

Further Researches.

The following researches were directed towards confirming, correcting and answering the facts and queries lettered above.

A and B. To test these observations more narrowly several hundred individuals were selected of a certain size (34·39—41·63 μ). A part of these were

killed, stained and their nuclei counted. Fig. A. The other part was put to encyst at room temperature 15°—19° C. with the result shown in Fig. B. From these figures the proportion of nuclei retained for encystment at room temperature by individuals of the above size can be fairly accurately gauged. The number is somewhat lower than previous observers have found; but it will be shown that the number of nuclei retained is greatly dependent on temperature.

C. When an *Actinosphaerium* builds few cysts for its size then the cysts tend to be small, and *vice versâ*.

If reference be made to Table III. which refers to the cysts built at room temperature, a complete confirmation of this rule will be obtained. This table was made up from those individuals used for constructing Fig. B whose cysts could be conveniently measured: the measurements refer to the diameter of the conjugation cysts. This table expresses the correlation between the number of cysts and the size of the cysts. The correlation coefficient $= -0{\cdot}6689 \pm {\cdot}0402$. The standard deviation of the numbers of cysts $= 1{\cdot}7599$; that of the sizes of the cysts $= 2{\cdot}3487 \times {\cdot}3\mu$. It will be seen that we have a most substantial negative correlation.

TABLE III.

Number of Cysts at 15°—19° C.

Diameter of Conjugation Cysts in μ.	1	2	3	4	5	6	7	8	Totals
5·2	—	—	—	—	—	—	—	—	—
5·5	—	—	—	—	—	1	—	—	1
5·8	—	—	—	—	—	—	—	—	—
6·1	—	—	—	1	—	—	—	—	1
6·4	—	—	—	—	—	—	—	1	1
6·7	—	—	—	—	—	—	—	—	—
7·0	—	—	—	—	—	1	1	2	4
7·3	—	—	1	1	—	2	4	—	8
7·6	—	—	3	2	8	2	2	1	18
7·9	—	—	6	4	2	3	1	—	16
8·2	—	2	8	4	5	—	—	—	19
8·5	—	8	4	2	—	—	—	—	14
8·8	—	—	1	—	—	—	—	—	1
9·1	—	1	—	—	—	—	—	—	1
9·4	—	—	—	—	—	—	—	—	—
9·7	—	—	—	—	—	—	—	—	—
10·0	—	—	—	—	—	—	—	—	—
10·3	1	—	—	—	—	—	—	—	1
10·6	—	—	—	—	—	—	—	—	—
10·9	1	—	—	—	—	—	—	—	1
Totals	2	11	23	14	15	9	8	4	86

Since the cysts built by one and the same individual are not always of exactly the same size I have had to average the size of the cysts in each individual. This applies to the whole table. The difference in size of the cysts built by any one individual was frequently nothing and only in two or three cases more than

FIG. B.
128 Individuals encysted at temperature of room.

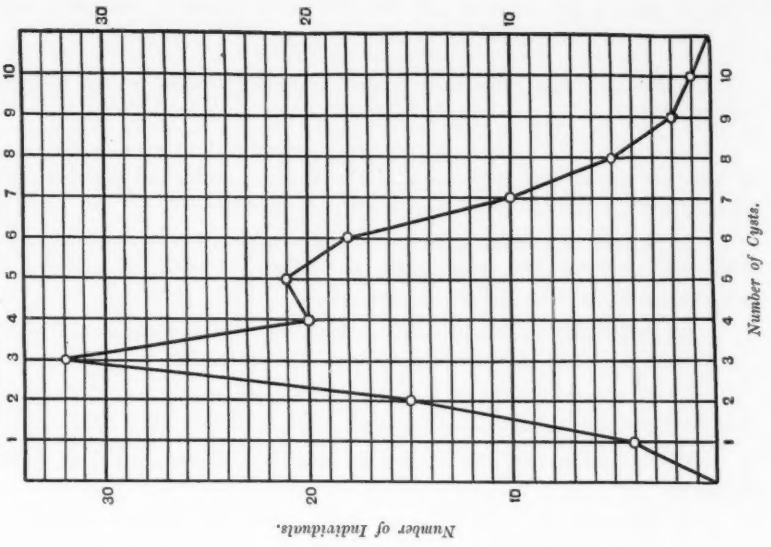
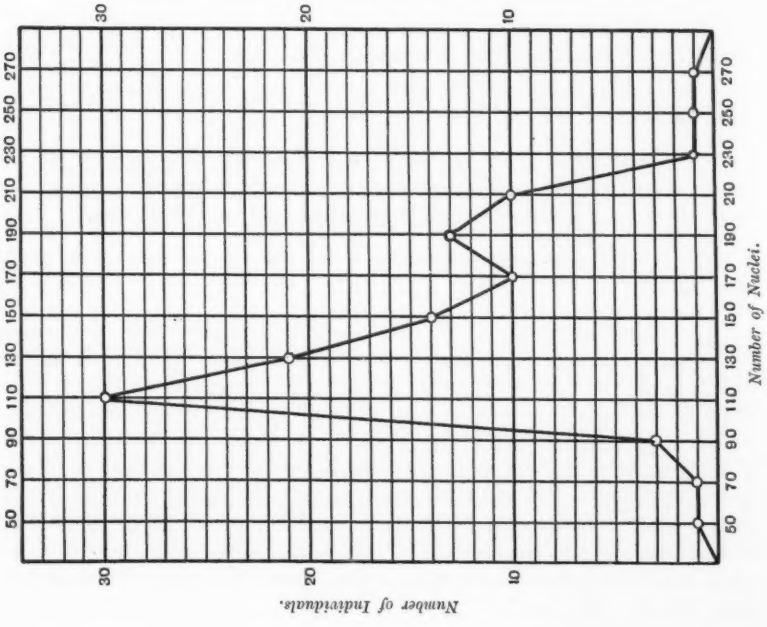


FIG. A.
106 Individuals.



half an unit of the scale, so that the process of averaging was only employed to cover small fluctuations.

D. An increased temperature hastens on encystment, a low temperature retards it.

I have proved the truth of this general statement by numerous instances but I have not determined the facts with the accuracy which the question deserves. The following rough observations must at present suffice:—

1. Individuals measuring 34·39—41·63μ were placed in the warm temperature (24°—26° C.) on Saturday evening 8th; on following Wednesday afternoon, 12th, conjugation cysts were formed in most cases.

2. Similar culture to above was set on 8th at room temperature (15°—19° C.); encystment began on 12th, conjugation cysts formed on 17th.

3. Similar culture to above placed in the cold temperature (7°—12° C.) on the 8th; encystment began on 19th, conjugation cysts formed on 23rd.

4. Culture at 24°—26° C. set on Saturday, all conjugated on following Thursday.

5. Culture at 24°—26° C. set on Sunday, all conjugated following Saturday.

6. Culture at 24°—26° C. set on 23rd, all conjugated 30th.

7. Culture placed in cold temperature (7°—12° C.) from Nov. 23rd—Dec. 2nd. Put in warm Dec. 2nd, all conjugated Dec. 8th.

8. Culture set at 7°—12° C. on Dec. 2nd, conjugation cysts formed on Dec. 16th.

From these facts it may be concluded that in starvation cultures the time of onset of encystment is directly dependent on the temperature, being quickest in the heat, intermediate at room temperatures, and much protracted in the cold.

E. An increased temperature causes fewer and larger cysts to be built, and *vice versâ*.

The reader must refer to Table IV. Here I have tabulated the correlation between the number of cysts and the size of cysts at 24°—26° C. with thin Arabic figures, while the Arabic figures in brackets refer to creatures that encysted in the cold 7°—12° C. It will be seen that the majority of the Arabic figures fall in the lower left-hand quarter of the table, i.e. the quarter referring to few and large cysts, while the figures in brackets fall in the upper right-hand corner, the quarter referring to numerous and small cysts. The figures in Table III. would form a kind of bridge between the two series in Table IV. The somewhat wide deviation from the mean exhibited by certain individuals that encysted at a high temperature suggests further problems: but the small number of instances do not permit of generalization.

TABLE IV.

Number of Cysts.

Diameter of Conjugation Cysts in μ.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Totals
5·2	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	1
5·5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5·8	—	—	—	—	—	—	—	—	—	(1)	—	—	—	(1)	2
6·1	—	—	—	1	—	—	—	—	—	—	(1)	—	—	—	2
6·4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6·7	—	—	—	—	—	—	(2)	(1)	—	—	—	—	—	—	3
7·0	—	—	—	5	(1)	(1)	(2)	—	(1)	—	—	—	—	—	10
7·3	—	—	—	I.	I. 1	(1)	—	—	—	—	—	—	—	—	4
7·6	—	II. 2	3	1	I. 1	I. 1	—	—	—	—	—	—	—	—	12
7·9	—	4	I. 1	(1)	1	—	—	—	—	—	—	—	—	—	8
8·2	—	I. 3	IV. 2	1	—	—	—	—	—	—	—	—	—	—	11
8·5	I. 1	I. 5	2	—	—	—	—	—	—	—	—	—	—	—	10
8·8	1	I. 7	—	—	—	—	—	—	—	—	—	—	—	—	9
9·1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	2
9·4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	2
9·7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10·0	—	I. 1	—	—	—	—	—	—	—	—	—	—	—	—	2
10·3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	3
10·6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10·9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Totals	9	29	13	10	6	4	4	1	1	1	1	0	1	1	81

Arabic figures refer to individuals encysted at 24°—26° C., Arabic figures in brackets to individuals encysted at 7°—12° C., Roman letters to individuals starved in the cold and introduced into the warm.

F. In what way does the temperature act upon the number of nuclei rejected?

It is plain that the temperature may act in one of two ways; either it may gradually increase or decrease the number of nuclei before encystment sets in, or else it may have no effect during this period but only at the actual onset of encystment, when the nuclei are being rejected. That this latter alternative is the truth is shown by the following experiments.

1. A culture was put to starve in the cold (7°—12° C.) on Nov. 23rd. It was introduced into the warm temperature (24°—26° C.) on Dec. 2nd, none of the creatures having as yet begun to encyst. On Dec. 8th conjugation cysts had been formed by all the individuals. The result is shown in Table IV. by the Roman letters. Here we see that whatever effect the application of cold under starvation for nine days may have had is obliterated by the subsequent application of warmth, for the Roman letters fall indifferently among the Arabic which refer to ordinary warm encystments.

2. Individuals of various sizes were well fed with Stentor in the cold. Half of them were killed and stained and found to be very rich in nuclei. The other half were introduced into the warmth on Dec. 7. On the following day they

had begun to encyst. The three individuals which were allowed to reach the conjugation stage had cysts of the following dimensions:

(*a*) 1 cyst = 8·31 μ, 15 cysts = 8·75 μ.
(*b*) 2 cysts = 8·75, 1 cyst = 8·31.
(*c*) 4 cysts = 8·31.

The cysts built by these individuals, then, were all large (cf. Table III.): from which we may safely judge that they were few in relation to the organisms' size. And yet we have seen that the organisms possessed many nuclei after being fed in the cold: but this seems to have had no effect in determining how many nuclei should be preserved for the process of encystment. This experiment shows in a striking manner that it is the temperature at the time of encystment which determines to an overmastering degree the number and in consequence the size of the cysts to be formed.

3. As the corollary to the above two experiments I may mention that I killed and stained the non-encysted weedings from both hot and cold starvation cultures in numerous instances, but was never able to find the slightest evidence that an increase of nuclei had taken place in the cold or a decrease in the warmth, in such a way that by this means the different numbers of nuclei retained for encystment in the two cases might be accounted for.

G. In what way does the size of the cyst affect the nucleus (chromatin) contained?

I must preface the following section, which constitutes the crucial part of the investigation, by drawing a distinction between the nucleus as a morphological entity and the chromatin as a physiological entity characterizing the former. We are not concerned here with a change of size of the nucleus as a morphological structure, a change which could be brought about by an alteration in the conditions of tension in the cell without any deeper changes in the physiological relations. But we are concerned with a change in the relative proportions of chromatin, the distinctive property of the nucleus, to the cytoplasm; and the question to be answered is, In the different sized cysts does the chromatin remain of a constant mass so that a different relation of chromatin and cytoplasm is to be observed in the different sized cysts, or has the cell the power of readjusting the relation between chromatin and cytoplasm? The reader must turn to Plate II. for an answer. These figures, drawn to scale, represent sections* through conjugation cysts built in the warmth, Plate II., in the cold, Plate III., and at room temperature, Plate IV.

* Owing to the opacity of the cysts I was obliged to cut sections of them in all cases. The thickness of the cyst coats makes them very difficult to preserve. I first used Picroacetic acid which distorts the cytoplasm (Figs. α—γ), subsequently I used Perenni's fluid which is more satisfactory (Figs. δ—ζ'), the fact that the cytoplasm in Figs. α—γ is distorted does not affect the relation of chromatin to cytoplasm; the size of the cyst may be roughly judged by the outline of the cyst coat and the mass of chromatin would not be altered by the preserving fluid used. Purists in Histology may neglect Figs. δ—ζ', and convince themselves of the main truth of the argument by the similarly ill-preserved figures.

A comparison of Figs. a'—g''' with Figs. 1—4′ shows that the mass of chromatin does not alter in correspondence to the different sizes of the cysts. In Figs α—ζ' which represent cysts built in the warmth, it appears that the amount of chromatin is absolutely as well as relatively less than in the other cases. It also tends to be more scattered.

(N.B. Where the chromatin lumps extended over more than one section they have been included in the figure.)

From the evidence that can be gleaned from Plates II. III. IV. the following rule may be formulated:—*Actinosphaeria* encysting under different temperatures exhibit a different mass relation between chromatin and cytoplasm, in the cold the chromatin being in excess, in the warmth the cytoplasm being in excess.

Conclusion.

Attention has been called to certain facts in the encystment of *Actinosphaerium Eichorni*. Of these the most important is that a different mass relation of chromatin and cytoplasm may be induced in the unicellular cysts by the application of heat and cold.

From the different sizes of the cysts formed under similar conditions of temperature, and from the widely different number of nuclei contained by free living *Actinosphaeria* of similar sizes and living under similar conditions of temperature, it must be judged that temperature is not the sole cause of this relation between chromatin and cytoplasm: analogy and a few facts given above point to nutrition as constituting the other chief cause. Whether the rule that warmth diminishes the amount of chromatin in proportion to the cytoplasm and that cold increases it will prove to be of at all wide application it is impossible to say from the absence at present of parallel experiments: experiments on this head are now being made by Professor Hertwig at Munich which seem to point to similar but wider conclusions. It is permissible to suggest that a deeper research into this and kindred problems may reveal facts which will throw a light upon the physiological differentiation of sex.

EXPLANATION OF PLATES II. III. AND IV.

Plate II. Figs. α—ζ'. Sections through conjugation cysts built in the warm (24°—26° C.). Note that in δ the nuclei are not yet fused.

Plate III. Figs. a'—g'''. Sections through the conjugation cysts built in the cold (7°—12° C.).

Plate IV. Figs. 1—4′. Sections through conjugation cysts built at room temperature (15°—19° C.).

In all cases the figures bearing the same letter or number are from cysts produced by the same *Actinosphaerium*.

All figures drawn accurately to scale under Zeiss objective DD, eye-piece 4.

si = siliceous cyst wall.
cy = cytoplasm.
chr = chromatin.

PLATE II.

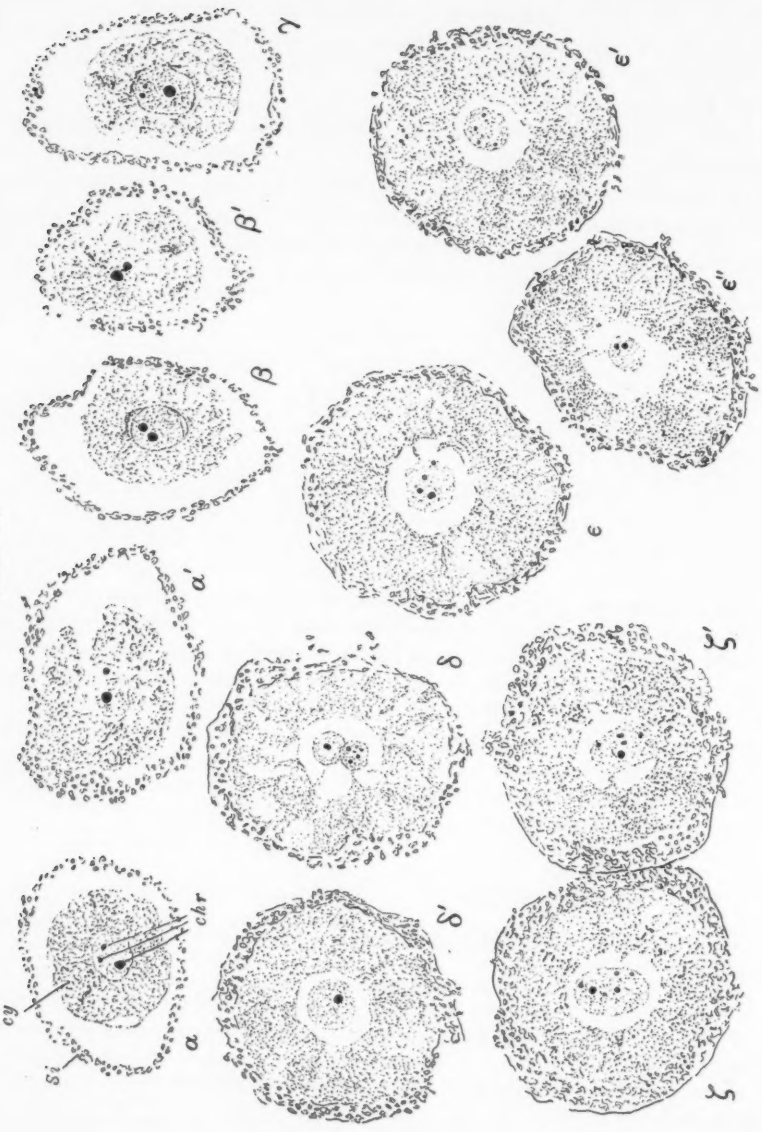


PLATE III.

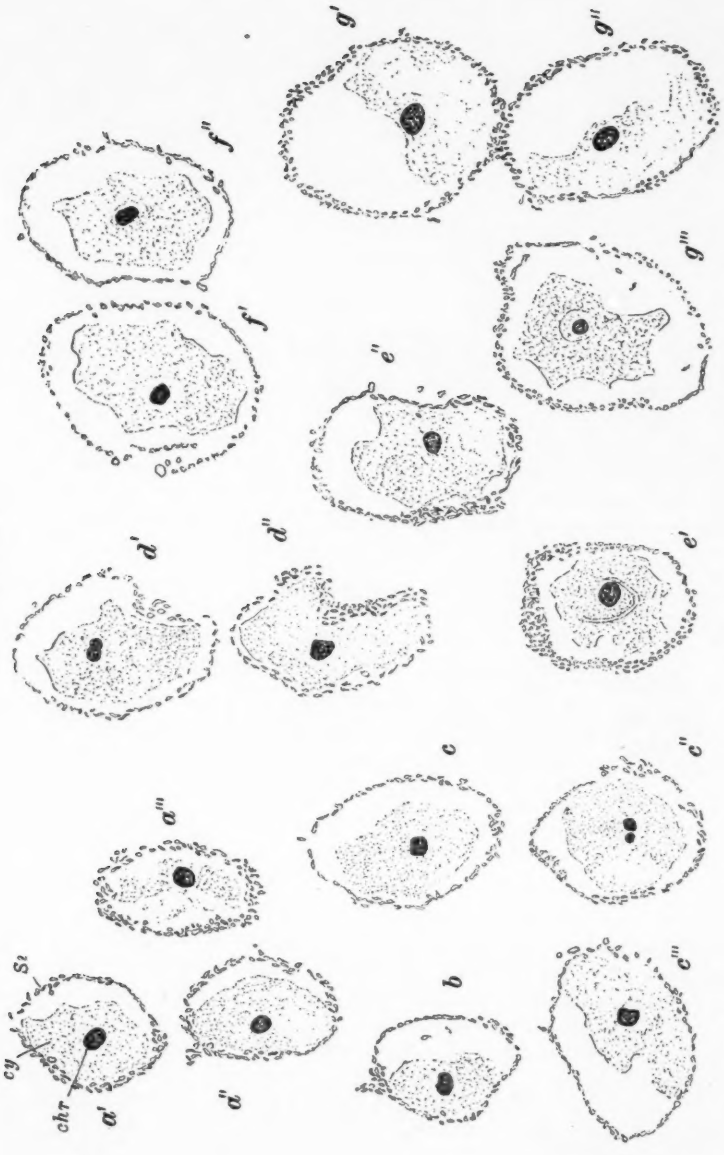
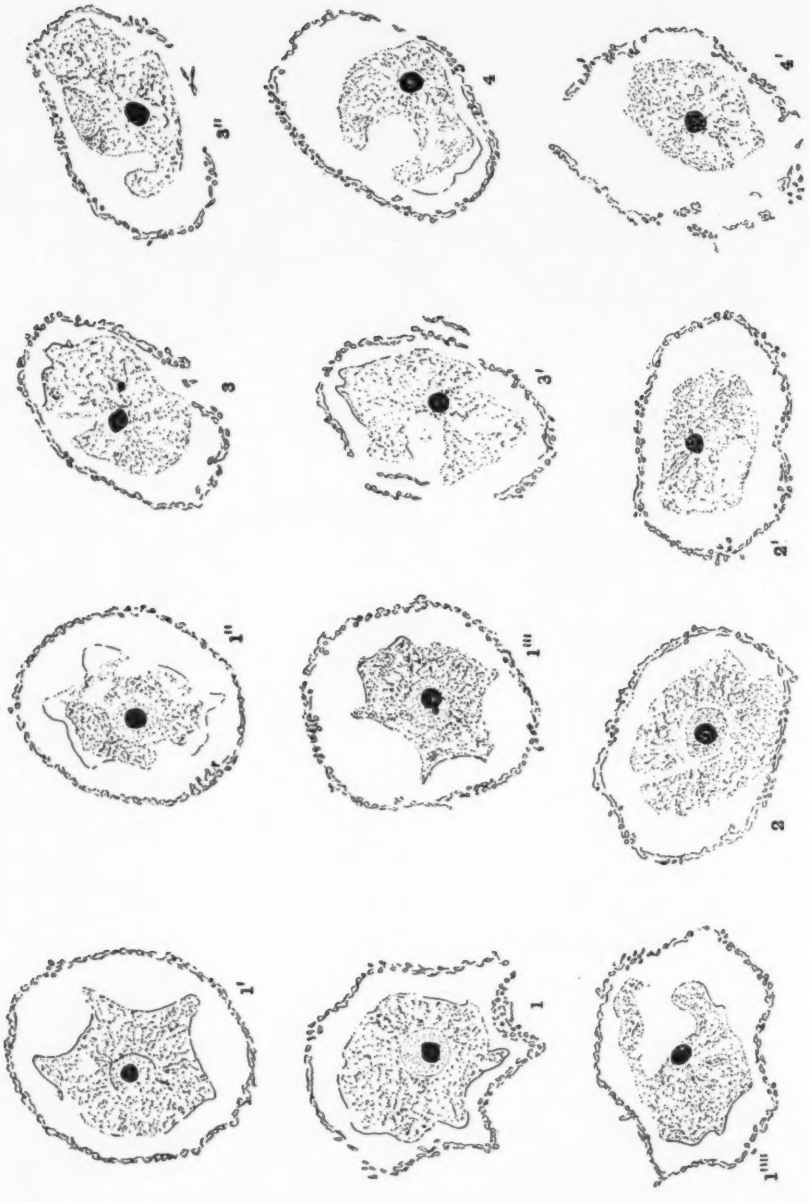


PLATE IV.



A PRELIMINARY ATTEMPT TO ASCERTAIN THE RELATIONSHIP BETWEEN THE SIZE OF CELL AND THE SIZE OF BODY IN *DAPHNIA MAGNA* STRAUS.

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In the course of investigating the development of the trematode of the crayfish (*Distomum corrigerum*) it was observed that the nuclei of the general body cells of the developing animal were very much smaller than those of the fully-grown creature. On comparing animals of different ages it could be readily seen that as the body grew as a whole so the individual cells became gradually larger.

According to the usual view that cells are units of very great individuality, growth of the body would imply *à priori* simply an increase in the *number* of these units and not a change in their mean size or general character.

Although in the case of the trematode there was no doubt about the intimate relationship between the size of the body and the size of the cell during a certain period of growth, yet it was desirable to ascertain whether there was a similar relationship in an actively growing animal of practically adult structure and not merely in a developing embryo.

For this purpose *Daphnia* appeared to be a suitable subject if some measurable cell character could be found in the fresh animal.

The surface of the carapace of *Daphnia magna* is covered with diamond-shaped areas which correspond with considerable exactitude to the cell-outlines of the underlying epidermal cells. A number of daphnia of various sizes were treated with picrocarmine. The free picric acid fixed the tissues to a certain extent, and the nuclei of the epidermal cells were sometimes, although by no means always, stained a very pale pink. It was then seen that typically one nucleus occurred under each area. Fairly frequently, however, but especially under any irregularly shaped areas two nuclei could be seen. In such cases the polygonal area would correspond to two epidermal cells. It was particularly noticed that the occurrence of two nuclei under an area could be observed as frequently in young and small individuals as in older and larger specimens.

The diameters of the diamond-shaped areas of the carapace are therefore regarded as giving us a conception of the sizes of the epidermal cells of that region. Only regular diamond-shaped areas were measured and in this way most of the measures would strictly correspond to cells. The fact that in some cases there may have been unavoidably included areas corresponding to two cells will not affect the comparative results because such would occur as often in the young as in the fully-grown animals.

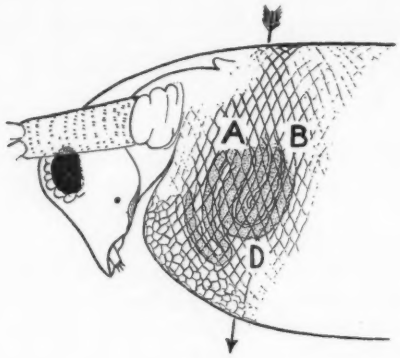


Fig. 1.

The dimensions taken were:

(1) The length of the body, measured from the anterior convexity of the head in front of the compound eye to the base of the dorsal spine.

(2) The diameters of 10 diamond-shaped areas over the middle lobe of the maxillary gland, and measured in the vertical direction. (See Fig. 1, *ABD*, the arrow indicates the direction of measurement.)

The daphnia were taken from a large tank at University College, London, and 201 animals of varying sizes were measured.

The measurements were made with an ocular micrometer, and under such magnification that a division of the micrometer scale in measuring the body-length was = 0·0320 mm., and the cell-length = 0·00385 mm.

The accompanying table gives the correlation surface for the length of daphnia and diameter of carapace cells. For the working scale the unit of length for the body was five divisions of the ocular micrometer = 0·160 mm., and for the cell dimension = 0·01925 mm.

The line of means for the arrays is represented in the annexed diagram. There is clearly a considerable correlation between the size of the body and the size of the cells, and this correlation is much greater at the younger periods of growth than it is at any later period.

Correlation Table of Body and Cell Lengths.

Body Length		Size of Cell	50—54	55—59	60—64	65—69	70—74	75—79	80—84	85—89	90—94	95—99	100—104	105—109	110—114	115—119	120—124	125—129	130—134		
		Working Scale	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Totals	Cell Means
32— 36		1	—	—	1	2	9	6	2	—	—	—	—	—	—	—	—	—	—	20	5·3000
37— 41		2	1	2	8	19	37	34	23	15	10	1	—	—	—	—	—	—	—	150	5·8333
42— 46		3	—	—	1	2	5	13	23	25	13	11	7	—	—	—	—	—	—	100	7·7900
47— 51		4	—	—	—	3	7	13	13	11	6	15	8	4	—	—	—	—	—	80	8·0500
52— 56		5	—	—	2	2	5	9	11	29	28	16	13	13	9	7	3	3	—	150	9·4733
57— 61		6	—	—	—	2	6	9	23	33	29	17	20	—	1	—	—	—	—	140	8·4357
62— 66		7	—	—	—	3	12	19	34	43	41	37	26	11	4	—	—	—	—	230	8·5957
67— 71		8	—	—	—	—	—	3	8	11	18	28	20	16	11	2	3	—	—	120	10·2667
72— 76		9	—	—	—	1	3	6	8	12	24	26	29	26	22	14	3	6	—	180	10·7611
77— 81		10	—	—	—	—	1	3	11	17	16	17	21	19	12	17	8	5	3	150	11·0267
82— 86		11	—	—	—	—	—	1	8	13	27	25	20	14	17	10	8	4	3	150	10·9533
87— 91		12	—	—	—	2	4	2	17	25	31	30	16	9	4	—	—	—	—	140	9·1000
92— 96		13	—	—	—	—	6	8	11	19	27	21	17	10	1	—	—	—	—	120	9·0000
97—101		14	—	—	—	—	1	4	22	19	34	49	45	27	11	5	3	—	—	220	10·0364
102—106		15	—	—	—	—	—	1	2	6	6	15	15	13	2	—	—	—	—	60	10·3167
Totals			1	2	12	36	96	131	216	278	310	308	257	162	94	55	28	18	6	2010	

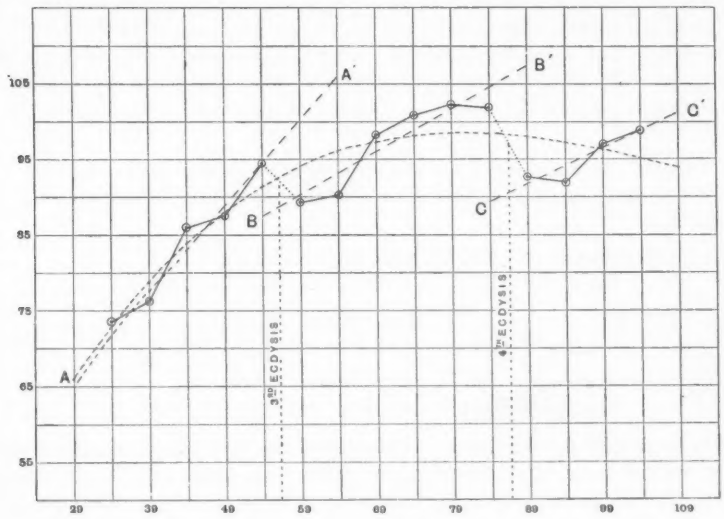


FIG. 2.

In this line of means two pronounced irregularities can be observed, one in the neighbourhood of a body length of 57—66 and one between 87—96. These mark

the positions of the 3rd and 4th ecdyses. In these daphnia the body length at the 1st ecdysis was about 36 units, at the 2nd about 48, at the 3rd 57—61, at the 4th 77—91; after the 4th shedding the animal generally produces eggs in the brood pouch and there is an indefinite number of ecdyses varying according to the length of life.

It might perhaps be objected that the measurements of the polygonal areas of the carapace simply indicates the amount of stretching of the exoskeleton between successive moults and that the cells divide underneath quite independently of them. But if this were so the number of nuclei under each area would gradually increase as the animal approached its next moult. An examination of a number of individuals did not, however, support this view and it appears that not until the creature is on the point of moulting do the cells divide to any extent, and then it is clear from a glance at the diagram that the divided cells are larger than the cells which occurred immediately after the previous ecdysis, i.e. the mean of the cells in array 87—91 is higher than that of array 57—61.

In the diagram the lines of correlation are drawn through three successive periods of growth (1) the period from the time of hatching to the time when the 3rd moult is about to take place, (2) the period from the 3rd moult to the 4th moult, (3) the period after the 4th moult has occurred.

Since the individuals are grouped simply according to the size of the body these periods will considerably overlap, for the size of the animal at which the different ecdyses take place varies very considerably from animal to animal. This overlapping of the different periods of growth produces a disturbing element which is especially noticeable in the array 82—86 and it obliterates the destruction which otherwise should be observed between the periods of the 1st and 2nd ecdyses.

If we make allowance for this disturbing element it must be agreed that the means of the arrays cluster fairly well around the three lines of correlation; the constants are *

(1) Correlation $r = \cdot5505$; Regression $= 1\cdot1337$;
Regression line: $y - 3\cdot4200 = 1\cdot1337\,(x - 7\cdot6500)$†.

(2) Correlation $r = \cdot3930$; Regression $= \cdot5851$;
Regression line: $y - 8\cdot4329 = \cdot5851\,(x - 9\cdot9217)$.

(3) Correlation $r = \cdot2477$; Regression $= \cdot4813$;
Regression line: $y - 13\cdot3704 = \cdot4813\,(x - 9\cdot5944)$.

It will be seen that the regression is greatest at the first period of growth and least at the third period, that is the size of the constituent cells is less closely related to the size of the body in the older than in the younger periods of growth.

* I am greatly indebted to Dr A. Lee for most kindly calculating these constants; and also those of the parabola to be mentioned below.

† y is the mean cell-length, x the body-length, both measured in the working scale units of the correlation table on p. 257.

If we now disregard the effect of ecdysis we can fit a continuous curve to the observations. A parabola of the 3rd order is shown in the diagram, the equation to it is:

$$y = 9{\cdot}0807\ \{1{\cdot}09787 + {\cdot}024{,}125x - {\cdot}005{,}992x^2 + {\cdot}000{,}228x^3\},$$

where the origin is at body-length 8 on working scale (observed cell mean 10·27), the unit of x, or the body-length, is five divisions of ocular micrometer used for body-length, and of y, or the mean cell-length, five of the divisions of the ocular micrometer used for cell-length (see p. 256).

An examination of this parabola shows us that the regression between size of body and size of cell, i.e. the slope of this curve, is very considerable at the younger periods but that this regression rapidly lessens as the animal grows older; there is also a distinct tendency for a negative regression to occur after the array 72—76*. This would mean that up to a certain period of life after the animal has been hatched, the cells of the carapace grow larger as the body grows, and that after this period has been passed the cells on dividing never again attain to such large dimensions. It leads to the question how far the period of life of maximum cell-size is to be regarded as the period of maximum vitality.

In the development of an animal (excluding the influence of yolk) the egg-cell divides into smaller and smaller cells and as the morula as a whole grows the constituent cells become smaller and the regression between the size of body and the size of cell is consequently negative. The cells reach a *minimum* size, and then in the developing distomum after a pause the regression becomes positive and the cells attain their *maximum* dimensions. Afterwards, in the case of daphnia and perhaps generally, there follows a slight negative regression.

It would be interesting to ascertain in a series of forms whether these are general phenomena, and if so, to find the point in the developing embryo at which the positive correlation becomes changed into a negative one, also the point of maximum cell-size in the actively growing animal. Perhaps these points might vary for different tissues or organs of the body or they might be nearly uniform throughout the whole body.

The essential feature of this preliminary note is to demonstrate the fact of the intimate relationship which obtains between the body as a whole and its constituent cells, the mean diameters of the cells change *pari passu* with the growth of the body.

There can be no doubt that a wider statistical study into the subject of cellular characters would yield results of fundamental importance both with regard to the laws of growth, and to our conceptions of the individuality of the cell-unit in the body of the living organism.

* Other curves were tried for graduating the observations, but the graduated values found for them were remarkably close to the present, and they shewed in the same way the like tendency to an ultimate reduction in cell size. The term regression is here used for the slope of the tangent to the curve which graduates the relation between body-length and mean cell-size, when we ignore the ecdysis effects.

GRADUATION AND ANALYSIS OF A SICKNESS TABLE.

By W. PALIN ELDERTON, *Actuary.*

"The whole problem of evolution is a problem in vital statistics—a problem of longevity, of fertility, of health and of disease." *Biometrika*, Vol. I. p. 320.

I.

Graduation by Frequency Curves.

The Report by the late William Sutton to the Chief Registrar of Friendly Societies in 1896 contains between one and two thousand pages of statistics dealing with the rates of sickness and mortality experienced by Friendly Societies in England and Wales between the years 1856 and 1880. On pages 1134—1151 a table of the rates of sickness for 1876—1880 (excluding the first three years of membership) is given which, Professor Pearson suggested to me, might afford an interesting study in graduation. Some graduated figures are given on pages 1167—1171 of the report but though they are referred to on p. xiv. of the Introduction the method by which they were obtained is not described. The ungraduated rates of sickness are obtained by dividing the number of weeks' sickness for the year of age by the number of persons of the same age exposed to the risk of being sick.

When an attempt is made to graduate a rate of sickness or mortality by a formula we may consider that we are trying to fit a curve to the actual number of weeks' sickness or deaths on the assumption that the number exposed to risk is unity at each age. Of course, this is an imaginary state of affairs and there seems little reason for adopting it in preference to taking some algebraic or trigonometric curve to represent the exposed to risk and then working on the amount of sickness or number of deaths obtained from the hypothetical series by multiplying its successive numbers by the ungraduated rates of sickness or mortality for the appropriate ages; or, we might adopt the opposite process and assume a curve for the sickness or deaths and graduate the exposed to risk. To

illustrate this proposition we may consider Gompertz' "Law of Mortality," which assumes that the force of mortality ($-\frac{1}{l_x}\frac{d}{dx}l_x$, where l_x is the number of persons living at age x in a stationary population) is of the form Ac^x and from the point of view taken above we can describe the "law" as assuming that if the exposed to risk be represented by the normal curve of error then the deaths will be represented by a curve of the same type having the same standard deviation. For the force of mortality is equal to the ordinate of the deaths divided by the ordinate of the exposed; this gives us $\kappa e^{-(x^2-x^2+hx-h^2)/2\sigma^2} = Bc^x$.

If possible, I think it would be a good principle in graduation to work on the exposed to risk and deaths (or weeks' sickness), for these functions are actual frequencies, but it is often difficult to do this in practice. In the present case, for instance, the exposed to risk for ages 18—22 are 3114; 4029; 5350; 23485; 33534 and this sudden change in the size of the numbers is awkward to deal with; nor is this the only difficulty, for though the exposed curve rises to a maximum at age 28 and then steadily falls, the sickness curve has two distinct maxima at ages 38 and 67.

A first examination of Sutton's table was made by assuming the normal curve of error as a hypothetical exposed to risk. The reason for choosing a frequency curve was that I have found it possible to represent (approximately) the exposed and deaths statistics in actual mortality investigations by such curves. The values for the integral $\left(\frac{2}{\sqrt{\pi}}\int_\tau^\tau e^{-t^2}dt\right)$ were found by taking equal intervals of ·06; this used the whole table given in Galloway's *Probability*. It was then necessary to decide on the origin for this curve. I wished to obtain, if possible, a frequency curve for the number of weeks' sickness derived from the hypothetical exposed and to avoid the two maxima of the sickness distribution referred to above. It was desirable, therefore, to have the mode of the exposed curve near the minimum of the sickness curve and this was obviously convenient for it was near the middle of the range. Age 52 was chosen as the origin. The amount of sickness was obtained by multiplying the areas of the normal curve $y = 67{\cdot}703\, e^{-x^2/2(11{\cdot}785)^2}$ by the rates of sickness and the resulting figures were grouped about every fifth age to render the calculation of the moments less laborious*. The grouped figures ran smoothly and were fitted closely by the Type I. frequency curve

$$y = 248{\cdot}34\left[1+\frac{x}{88{\cdot}67125}\right]^{13{\cdot}3230}\left[1-\frac{x}{37{\cdot}6809}\right]^{5{\cdot}8741},$$

with an origin at 64·269406. The graduated rates were unsatisfactory above age 85, as they decreased very rapidly owing to the sickness curve ending at 101·950.

The rates of sickness given in Fig. 1 were obtained by dividing the areas of the above-mentioned Type I. curve corresponding to each age by the areas of the

* An attempt to split up the distribution into two normal curves failed to give satisfactory results.

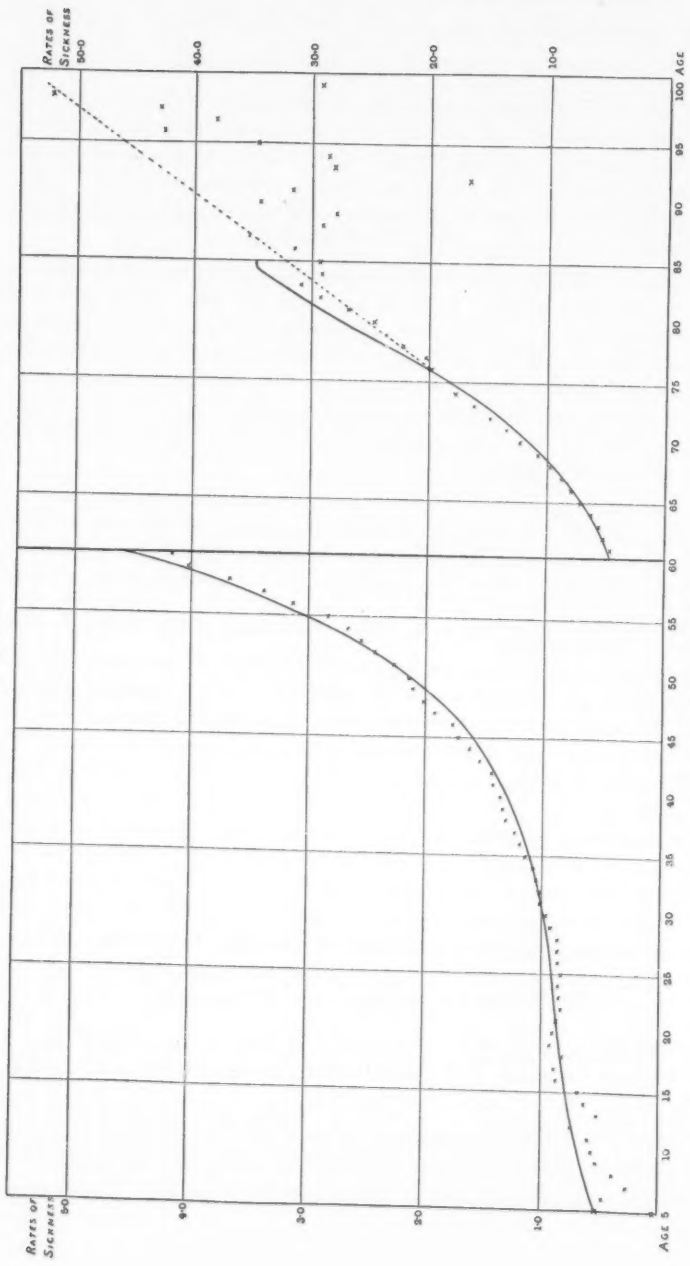

RATES OF SICKNESS
50·0
40·0
30·0
20·0
10·0
AGE
100
95
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
×××××
Ungraduated Rates of Sickness.
——
Graduated Rates of Sickness.
- - - - -
Continuation of Graduation by a Straight Line.

FIG. 1.

normal curve which had been already used for finding the actual amount of sickness to which the Type I. curve was fitted. Strictly speaking, I think it would have been more correct to read off ordinates in the denominators, but the analysis of the point can hardly be dealt with in a few lines, and would be of a technical character. The use of areas makes it impossible to write down an algebraic expression for the rates of sickness; the quotient of the ordinates of the two curves would not give these rates, but a function that might be called the "force of sickness," for it is analogous to the force of mortality mentioned above.

This result was so good that I decided to make some further trials in the hope of obtaining other interesting representations. Symmetrical limited-range curves were tried with the same origin but though nearly all the Type I. curves I obtained represented the amount of sickness closely they failed at the ends of the table to give a satisfactory graduation of the sickness rates. A few trials were also made with different origins.

The next attempts were made from the opposite point of view, that is, a hypothetical curve was assumed for the sickness. The same normal curve was tried and the exposed to risk were then represented by a Type IV. curve

$$y = 273{\cdot}3649\,[1 + x^2/(66{\cdot}9576)^2]^{-21{\cdot}00072}\, e^{-4{\cdot}4504\tan^{-1}(x/66{\cdot}9576)},$$

with an origin at 52·5043939. This curve is very nearly symmetrical but on trying a normal curve it was found to fail above age 66 (i.e. for 34 ages. Compare Makeham's "Law of Mortality" which is unsuitable for the first 25 ages). In order to see if the quotient of two normal curves would graduate the rates I tried to fit the parabola $y = a + bx + cx^2$ * to their logarithms but the result was unsatisfactory. Trials were then made with limited-range curves and the corresponding exposed to risk represented by Type I. curves. The results were unsatisfactory as regards the rates for at least 15 consecutive ages, in the case of the Type IV. and normal curve, for instance, the rates were considerably too low from age 67 to age 82. A trial with the Type I. curve to the rates of sickness also gave a poor result.

Viewed as processes of graduation the trials mentioned above are, as a rule, satisfactory for the main part of the sickness table and the practical conclusion to be drawn is that a rapid graduation can be made with reasonable results as far as age 80 or 85. The assumption of a hypothetical curve for the exposed is preferable to the opposite course, for, if the latter be adopted, there is some doubt as to the correct values to be given to the exposed to risk at ages where no persons have been sick. In the present case this only occurred at age 4, but in small experiences it would be a matter of greater importance. Another reason for the preference is that the old age end of the experience is relatively smaller when the hypothetical curve is used for the sickness than when it is used for the exposed; that is to say, the former method gives less weight to the old age values than the

* Rate of sickness $= ke^{-(x-h)^2/s_1} + e^{-(x-l)^2/s_2}$, therefore log rate $= ax^2 + bx + c$ (see Pearson, "On the Systematic Fitting of Curves," *Biometrika*, Vol. II. Pt. I.).

latter method, and, as we wish to graduate our rates as nearly as possible to the end of the table, the point is worth bearing in mind.

The first method I have described gave the best graduation and it could be improved by calculating the figures for the sickness to a few more places of decimals and using every term for finding the moments instead of groups of five. We might also treat the rate of sickness beyond age 100 as 52·167*; for by using an infinite-range curve as the exposed we assume that some live beyond the last age occurring in the experience and it is not unreasonable to suppose that they would be permanently sick. The rates for the last ten or fifteen ages if unsatisfactory might be altered by graduating the end of the experience by a parabolic curve or they might be supplied by drawing a straight line such as the dotted one shewn in the figure. I may remark, however, that for practical purposes it is unnecessary to obtain graduated rates of sickness right up to the limit of old age; in fact Bowser's tables† end (as regards sickness) at age 80 and he says on p. xv. of his Introduction that "if the rules of a society permit 'sick pay' to be "continued for the whole of life the valuer should regard the sickness benefit "after age 80, or still better age 75, in the light of a *Pension for life*" and his pension tables provide for the chronic sickness of old age.

For the present purpose it seems unnecessary to discuss the advantages of the method of graduation as it would involve a somewhat lengthy comparison with other methods which would have to be explained for non-actuarial readers; but it is obvious that the graduated rates must run evenly and will agree with the observed rates closely if the amount of sickness can be represented accurately by a frequency curve.

II.

Analysis of Sickness Table.

My object in continuing the work beyond a mere graduation of Sutton's Table was to see if sickness may be referred to certain broadly marked periods of life corresponding to those which Professor Pearson shewed were characteristic of mortality.

Before giving the work done in connection with sickness it will be well to recall the results obtained by Professor Pearson from his investigation of mortality. The function on which he worked was that known to actuaries as the "deaths" or "d_x" column of the mortality table‡. This column gives the number of persons

* 52·167 weeks was taken as a full year by Sutton; on p. xii. he says "it should be added that I "have invariably considered as regards broken weeks that there are six working days in a week."

† "Friendly Societies' Valuation and other tables deduced from the experience of the Independent "Order of Oddfellows, Manchester Unity Friendly Society, 1866—1870" by Wilfred A. Bowser. London, C. and E. Layton, 1896. The Manchester Unity table is the standard for Friendly Society Valuations.

‡ The reader must be careful to distinguish between the d column of the mortality table and the number of deaths in a mortality experience; the latter is the actual number who die, the former is a

who would die at each year of age in a stationary community supported by, say, l_0 births, or it may be considered as the number of persons who would die in each year of age out of l_0 persons born at the same time. When a mortality table is constructed the first function obtained is either the probability of living a year (p_x) or of dying during a year (q_x) at age x, and, since d_x is obviously equal to l_x (the number living at the exact age x) $\times q_x$ it is easy to see how the column d_x can be formed continuously from q_x.

In *The Chances of Death* (London, 1897)* Professor Pearson gave a description of his analysis of the "deaths" column of the mortality table (English, No. IV. Table) constructed by Dr Ogle from the Registrar-General's Returns for the years 1871—1880 and shewed that the old age part of the deaths curve could be represented accurately by a Type III. frequency curve having its origin at 71·5, that is, at the middle of the d_{71} group, and when this "old age" curve was deducted from the deaths curve the end of the remainder could be fitted by a normal curve having its origin at 41·5. This curve was called the "Middle life" curve and when it was deducted a "Youth" curve of the normal type with an origin at 22·5 was found. The rest of the deaths curve was fitted by a "Childhood" curve of Type III. with origin at age 3 and an "Infancy" curve which started 9 months before birth at infinity and was of the type $y_0 x^{-p} e^{-\gamma x}$.

Turning from Professor Pearson's work to the table we have graduated we notice at once that from a statistical point of view there is a great difference between mortality and sickness, for in the case of the former if a person dies he must, of necessity, pass out of observation, but a person may be sick, and, especially in the earlier periods of life, recover—that is, he does not cease to be a part of the experience under observation. For this reason we are obliged to alter our conception of a sickness table in order to obtain a function analogous to that used in the analysis of the mortality table. The rate of sickness at any age, as it is now used, is the average number of weeks' sickness falling to the lot of each person under observation at that age and if we divide this rate by 52·167† we get the average number of years' sickness, or *the probability* (r_x *say*) *that an individual will be sick for the whole year* under certain hypothetical circumstances arising from the assumption that persons are either sick for a whole year or not at all, and, having been sick for the whole year, pass out of observation altogether just as if they had died. The assumption is subsequent to the calculation of the sickness rates and it will not affect any results already obtained; our change of view merely accentuates the fact that we deal with the community as a whole and not with its individual members.

If we take h_0 persons at birth, then $h_0 r_0$ ($= f_0$ say) will represent the amount of sickness in years or the number of persons who are sick for the year of age (0—1)

purely hypothetical function tabulated for convenience, and they can only be connected by means of the rates of mortality. The same distinction must be made between the number of weeks' sickness and the f column.

* See also *Phil. Trans.* A, Vol. 186, p. 343.

† Number of weeks in the year assumed by Sutton (see footnote, p. 264).

on the assumptions involved in our altered arrangement of the table. If we continue the calculations remembering that $h_x = h_{x-1} - f_{x-1}$ and $f_x = h_x r_x$ we shall form an "f" column for sickness equivalent to the "d" column for death.

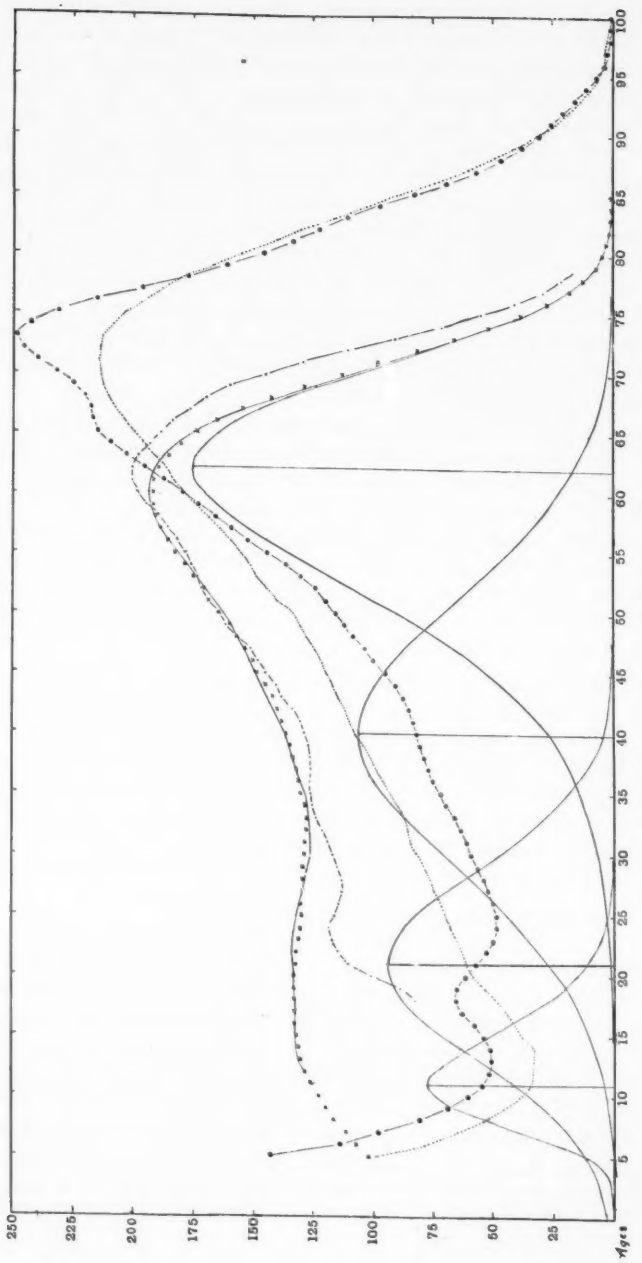
An "f" column was formed from the graduated rates of sickness and, as it appeared to shew some similarities to the "d" column, I proceeded to split it up into component parts beginning, of course, with the old age end of the curve. The equations found for the various curves and the corresponding numbers are given in Table II. and the curves drawn out (Fig. 2) but it would be unwise to place much reliance on the "Childhood" curve as the figures on which it is based are derived from comparatively few cases. Taking the curves in order, beginning at old age, we notice that the old age sickness curve is much steeper and has its origin some nine years earlier than the death curve relating to the same period of life. The normal curves representing the sickness in "Middle Age" and "Youth" have their origins a little earlier than the corresponding death curves for the English No. IV. table, but the difference is slight. In other words *on the average*, death, if it comes, follows quickly on sickness in early life, but in old age it may follow the modal age of sickness by even nine years. A noticeable character in the analysis of the sickness curve is that the proportion of sickness ascribed to the "Youth" and "Childhood" groups is much larger than the proportion of deaths which Professor Pearson found related to the equivalent death groups.

We have referred above to the fact that the old age sickness curve precedes the death curve and that the distance between them increases with the age; this is, of course, natural at the end of the table for sickness must come before death, and the curve for the latter will therefore become insignificant at a later age than the curve for the former. When we get nearer birth however it is not *necessary* for the origins of the sickness curves to be earlier than those of the deaths curves, for, if the rate of mortality is low (most obviously when it is decreasing) the fact of the sickness origin coming after the deaths origin would only indicate that the incidence of the sickness in the particular period of life was such that the sickness rate was increasing at a relatively greater rate than the death rates. The only thing that seems necessary is that the sickness curve for any group should not *start* later than the death curve.

I may here digress to refer to an auxiliary table which I found useful in splitting up the f column when the component part required a curve of Type III. The equation of a curve of this type may be expressed as

$$\log_{10} y_x = \log_{10} y_0 + \gamma \log_{10} (1 + x) - \gamma x \log_{10} e,$$

where the range on the side of the origin where the curve does not extend to infinity, is taken as the unit for x. Now since y_0 can be taken as unity the right-hand side of this equation may be written $\gamma [\log_{10} (1 + x) - x \log_{10} e]$ and a table of the function in square brackets was formed to six places of decimals for values of x from -1 to 2·5 with intervals of ·05. The use of such a table for finding γ and a is obvious and as it is also a help in calculating the actual curve when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×××××× Sutton's Sickness Table. Graduated, f column.
——— " " Split up by frequency curves, f column.
•—•—• Manchester Unity—Sickness Table (Bowser), f column.
o—o—o Sutton's Mortality Table, Sutton's Graduation, d column.
····· English No. IV. Table (l_x being taken as 10000).

FIG. 2.

γ and a have been found, the table is given below. The normal curves were obtained by comparing the column of first differences in the table of the integral in Galloway's *Probability* with the data to which it was required to fit the curve. The normal curve was tried in each case and when it failed to give a satisfactory representation a Type III. curve was substituted. The work was originally done with four figures and afterwards reduced to three and I made it a rule in finding my curves not to pass a difference larger than 30 when the figure in the "f" column was more than 1000, my reason for choosing the limit being that the square of the difference divided by the frequency is a measure of the goodness of fit, and I noticed that if each of these measures was about ·8 the fit would be very good. As will be seen from the table most of the differences were considerably smaller; the two differences entered as 3 for ages 23 and 24 lie between 2·5 and 3·0. The average difference shewn by the table is ·9 and this seems good evidence that though the method adopted was tedious it had the merit of bringing out a satisfactory result.

I have drawn out the "f" column obtained from the graduated sickness table and the values of the same function for the Manchester Unity table* are also given in the diagram. In order to bring out the connection between the "f" (sickness) and "d" (mortality) columns I have also shewn the "d" column obtained from the "l" column given on p. 1176 of Sutton's work relating to 10,000 living at age 5 and the same column from the English No. IV. table altered so as to give the same number living at age 5. The analysis of the "f" curve is also given. The ages at the bottom of the diagram are at the centre of the groups to which they refer; so that f_{30} is above age 30 not 30·5.

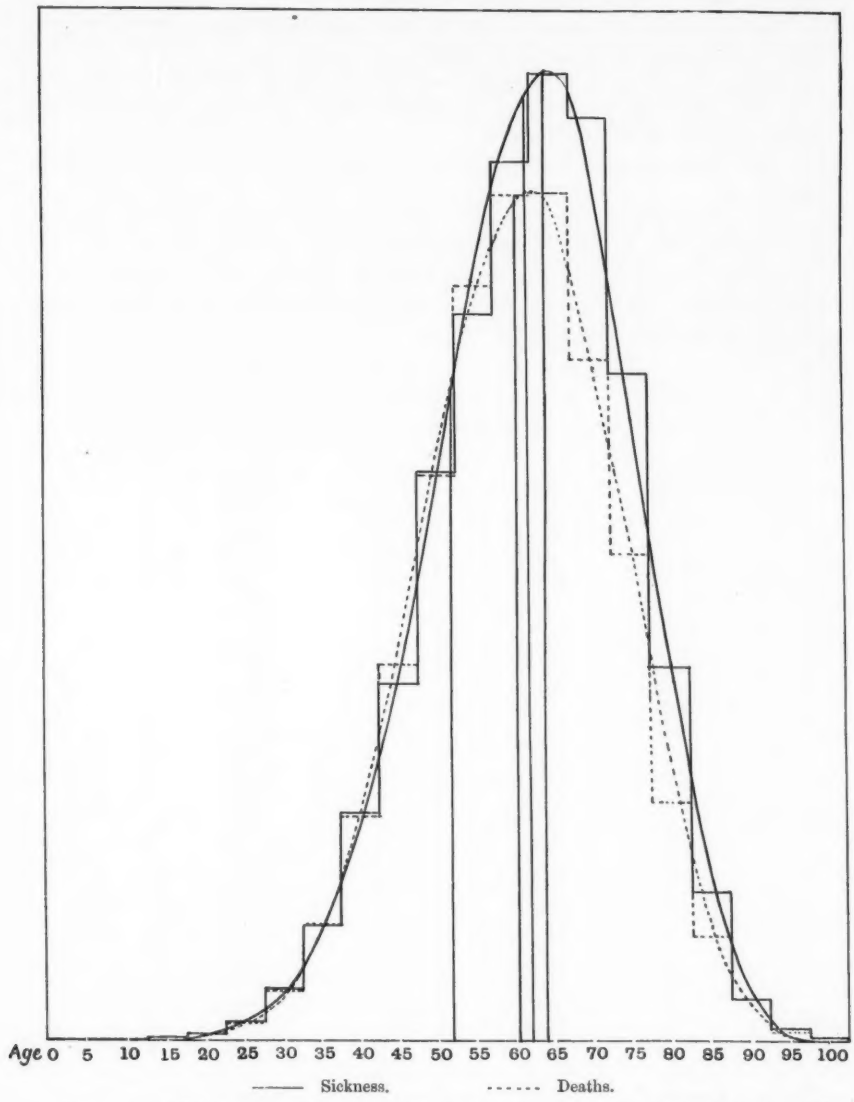
We may however view the comparison between the rates of sickness and mortality from the point of view of our sickness graduation and find the curve that will represent the number of deaths if the exposed to risk is the same series as that assumed in the sickness graduation. Mr Sutton in his Report gave a table of the ungraduated rates of mortality (from the graduated rates the "d" column referred to above was calculated) obtained from the same experience as that from which the sickness rates were found and I applied the method of graduation to these rates and found that the number of deaths could be represented

by $$y = 174{\cdot}19\left[1+\frac{x}{68{\cdot}0265}\right]^{10{\cdot}35195}\left[1-\frac{x}{43{\cdot}7927}\right]^{6{\cdot}68415},$$

having its origin at age 61·9319. To obtain this curve the areas of the normal curve were multiplied by the corresponding values of q_x by Crelle's Tables and not more than three figures were used in the products which were grouped in fives before the moments were calculated. These abbreviations saved a great deal of labour and though, combined with the irregularity of the data before age 20 and after age 75, they render the graduated rates somewhat unsatisfactory at the ends of the experience (probably above 87 and under 12) they would only

* When these values were calculated it was assumed that the value of h_{20} by the Manchester Unity table was the same as that given by Sutton's Sickness table. Some such assumption was necessary because Bowser's tables begin at age 20.

FIG. 3. *Amount of Sickness and Number of Deaths when the Exposed to Risk is represented by the same Normal Curve.*



Each square half-inch = 200 weeks' sickness = 160 deaths. The vertical lines taken in order from left to right shew (1) axis of normal curve giving exposed to risk, (2) mean of deaths, (3) mode of deaths coinciding to our scale with mean of sickness, (4) mode of sickness.

affect the main part of the table to a small extent and as the death curve was only required for comparison I considered it perfectly safe to use them.

The curve has been plotted side by side with the sickness curve in figure 3 and the following points may be noticed:—

(1) The skewness of the sickness curve is ·2 and of the death curve ·1.

(2) The mode and mean of the sickness curve are nearer old age than the mode and mean of the death curve.

(3) The sickness curve starts 18 years and ends 4 years before the death curve.

An examination of the two curves shews the connection between sickness, mortality and age and is perhaps the simplest way of doing so.

This concludes my work on Sutton's Table but the analysis of sickness will be very incomplete till other tables have been studied and infantile sickness has received a thorough examination.

TABLE I. (*for use with Type III. curves*).

X	$\log_{10}(1+X) - X\log_{10}e^*$	X	$\log_{10}(1+X) - X\log_{10}e^*$
−·95	·888450	+ ·80	·092163
−·90	·609135	+ ·85	·101979
−·85	·454759	+ ·90	·112111
−·80	·351534	+ ·95	·122545
−·75	·276339	+1·00	·133265
−·70	·218873	+1·05	·144255
−·65	·173641	+1·10	·155505
−·60	·137363	+1·15	·167000
−·55	·107926	+1·20	·178731
−·50	·083883	+1·25	·190685
−·45	·064205	+1·30	·202855
−·40	·048131	+1·35	·215230
−·35	·035084	+1·40	·227801
−·30	·024614	+1·45	·240561
−·25	·016365	+1·50	·253502
−·20	·010051	+1·55	·266616
−·15	·005437	+1·60	·279898
−·10	·002328	+1·65	·293340
−·05	·000562	+1·70	·306937
·00	·000000	+1·75	·320683
+·05	·000525	+1·80	·334572
+·10	·002037	+1·85	·348600
+·15	·004446	+1·90	·362761
+·20	·007678	+1·95	·377052
+·25	·011664	+2·00	·391468
+·30	·016345	+2·05	·406004
+·35	·021669	+2·10	·420657
+·40	·027590	+2·15	·435422
+·45	·034065	+2·20	·450298
+·50	·041056	+2·25	·465279
+·55	·048530	+2·30	·480363
+·60	·056457	+2·35	·495547
+·65	·064808	+2·40	·510828
+·70	·073557	+2·45	·526202
+·75	·082683	+2·50	·541668

* This column is negative throughout and as it will have to be multiplied it will be found more convenient to deal with the logarithms in this form than in the usual one giving a positive mantissa and negative characteristic.

TABLE II.

Ages	Descriptions of Curves: Old Age Origin 62·5 $175{\cdot}7\left(1-\frac{x}{25}\right)^{7\cdot15}e^{-{\cdot}286x}$	Middle Age Origin 40·5 $106{\cdot}0e^{-{\cdot}003844x^2}$	Youth Origin 21·5 $94{\cdot}1e^{-{\cdot}01235x^2}$	Childhood Origin 11·5 $77{\cdot}0\left(1+\frac{x}{10}\right)^{6\cdot2}e^{-{\cdot}62x}$	Infancy	Total by Curves	"f" column	Difference +	Difference −
85	·0	—	—	—	—	—	·1	—	—
84	·1	—	—	—	—	·1	·1	—	—
83	·3	·1	—	—	—	·4	·4	—	—
82	1	—	—	—	—	1	1	—	—
81	2	—	—	—	—	2	2	—	—
80	4	—	—	—	—	4	4	—	—
79	7	—	—	—	—	7	7	—	—
78	12	—	—	—	—	12	12	—	—
77	19	—	—	—	—	19	18	1	—
76	27	1	—	—	—	28	27	1	—
75	37	1	—	—	—	38	38	—	—
74	50	1	—	—	—	51	52	—	1
73	64	2	—	—	—	66	66	—	—
72	78	2	—	—	—	80	82	—	2
71	94	3	—	—	—	97	98	—	1
70	109	3	—	—	—	112	113	—	1
69	123	4	—	—	—	127	129	—	2
68	136	5	—	—	—	141	143	—	2
67	148	7	—	—	—	155	155	—	—
66	158	8	—	—	—	166	166	—	—
65	165	10	—	—	—	175	174	1	—
64	171	12	—	—	—	183	181	2	—
63	174	14	—	—	—	188	186	2	—
62	175	17	—	—	—	192	190	2	—
61	174	20	—	—	—	194	192	2	—
60	171	23	—	—	—	194	192	2	—
59	167	27	—	—	—	194	192	2	—
58	161	31	—	—	—	192	191	1	—
57	153	35	—	—	—	188	189	—	1
56	145	40	—	—	—	185	186	—	1
55	137	45	—	—	—	182	183	—	1
54	128	50	—	—	—	178	179	—	1
53	119	55	—	—	—	174	176	—	2
52	109	61	—	—	—	170	172	—	2
51	100	67	—	—	—	167	169	—	2
50	91	72	—	—	—	163	165	—	2
49	82	78	—	—	—	160	161	—	1
48	74	83	—	—	—	157	157	—	—
47	66	88	—	—	—	154	154	—	—
46	59	92	1	—	—	152	151	1	—
45	53	96	1	—	—	150	149	1	—
44	47	100	1	—	—	147	146	1	—
43	41	102	2	—	—	145	143	2	—
42	36	104	3	—	—	143	141	2	—
41	31	105	4	—	—	140	139	1	—

TABLE II.—(*continued*).

Ages	Descriptions of Curves					Total by Curves	"f" column	Difference	
	Old Age Origin 62·5 $175{\cdot}7\left(1-\frac{x}{25}\right)^{7{\cdot}15}e^{{\cdot}0286x}$	Middle Age Origin 40·5 $106{\cdot}0e^{-{\cdot}003844x^2}$	Youth Origin 21·5 $94{\cdot}1e^{-{\cdot}01235x^2}$	Childhood Origin 11·5 $77{\cdot}0\left(1+\frac{x}{10}\right)^{6{\cdot}2}e^{-{\cdot}62x}$	Infancy			+	−
40	27	106	5	—	—	138	137	1	—
39	24	105	7	—	—	136	135	1	—
38	20	104	9	—	—	133	134	—	1
37	18	102	12	—	—	132	133	—	1
36	15	100	16	—	—	131	132	—	1
35	13	96	20	—	—	129	131	—	2
34	11	92	24	—	—	127	129	—	2
33	10	88	30	—	—	128	128	—	—
32	8	83	36	—	—	127	128	—	1
31	7	78	43	—	—	128	129	—	1
30	6	72	49	—	—	127	129	—	2
29	5	67	56	1	—	129	130	—	1
28	4	61	64	1	—	130	130	—	—
27	3	55	71	1	—	130	130	—	—
26	3	50	77	2	—	132	131	1	—
25	2	45	83	3	—	133	131	2	—
24	2	40	88	4	—	134	131	3	—
23	2	35	92	6	—	135	132	3	—
22	1	31	94	8	—	134	133	1	—
21	1	27	94	11	—	133	133	—	—
20	1	23	94	16	—	134	134	—	—
19	1	20	92	21	—	134	134	—	—
18	1	17	88	27	—	133	134	—	1
17	1	14	83	35	—	133	134	—	1
16	1	12	77	43	—	133	134	—	1
15	—	10	71	52	—	133	133	—	—
14	—	8	64	61	—	133	132	1	—
13	—	7	56	69	—	132	131	1	—
12	—	5	49	75	—	129	129	—	—
11	—	4	43	76	2	125	126	—	1
10	—	3	36	74	10	123	123	38	38
9	—	3	30	67	20	120	120		
8	—	2	24	54	37	117	117		
7	—	2	20	39	51	112	112		
6	—	1	16	23	67	107	107		
5	—	1	12	11	78	102	102		
4	—	1	9	3					
3	—	—	7	1					
2	—	—	5						
1	—	—	4						
0	—	—	3						

On the Probable Errors of Frequency Constants.

(EDITORIAL.)

Introductory.

In all reasoning on statistical data we have to determine whether differences between statistical constants are significant or not. Half the blunders made in superficial statistical investigations arise from neglecting the values of the probable errors of the results obtained. But the calculation of probable errors becomes somewhat complex, when we have to deal not merely with the probable errors of means, but with those of constants depending in a much more intricate manner on the moments of the material.

The fundamental memoirs on the subject are W. F. Sheppard: "On the Application of the Theory of Error to cases of Normal Distribution and Normal Correlation," *Phil. Trans.* A., Vol. 192, pp. 101—167. L. N. G. Filon and K. Pearson: "On the Probable Errors of Frequency Constants and on the Influence of Random Selection on Variation and Correlation," *Phil. Trans.* A., Vol. 191, pp. 229—311.

The present discussion of the probable errors of frequency constants presents, perhaps, little that is novel, but it endeavours to give simple proofs of the main propositions of the subject. It is published in *Biometrika*, because several readers of that Journal have written to the Editors making enquiries on these points, recognising that the non-publication of probable errors in statistical memoirs is a serious disadvantage.

The simple idea involved in the probable error of a statistical constant is of the following kind: If the whole of a population were taken we should have certain values for its statistical constants, but in actual practice we are only able to take a sample, which should if possible be a "random sample." If a number of random samples be taken any statistical constant will vary from sample to sample, and its variation is distributed according to some law round the actual value of the constant for the total population. This variation would be very properly measured by the standard deviation of the constant for an indefinitely great series of random samples. Unfortunately custom has not taken this standard deviation as the measure of the goodness of the sample, but the whole theory having ultimately developed from the normal curve, the probable error instead of the standard deviation has been chosen, i.e. $\cdot 67449 \times$ standard deviation. The adoption of the "probable error" of a constant as a measure of its exactness must not, however, be taken as equivalent to asserting the validity of the normal law of errors or deviations, but merely as a purely conventional reduction of the standard deviation. It would be equally valid provided it were customary to omit this reduction or indeed to multiply the standard deviation by any other conventional factor.

PROBLEM I. *Let there be n frequency groups, containing in the total population of N individuals, $y_1, y_2, y_3 \ldots y_n$ individuals respectively. To find the standard deviation of y_s, when random samples are made of m individuals from the whole population.*

The chance of an individual being drawn from the s^{th} group on one trial $=\frac{y_s}{N}=p$ say, and of its not being drawn $=1-\frac{y_s}{N}=q$, say. Then in m trials the distribution of frequency of this group will be given by $(p+q)^m$, with the known standard deviation $\sigma_{y_s}=\sqrt{mpq}=\sqrt{m \cdot \frac{y_s'}{m}\left(1-\frac{y_s'}{m}\right)}$, where $y_s'=\frac{m}{N}y_s$ and is accordingly the proportion of y_s which we should expect in the typical group of m out of the N individuals. But in actual practice we have only the sample and do not know N or y_s. If y_s'' be the observed frequency of the s^{th} group y_s'' will almost certainly lie within $y_s \pm 3\sigma_{y_s}$. Hence in the above formula for σ_{y_s} we may replace, if σ_{y_s} be small compared with y_s, y_s' by y_s'', the observed frequency of the sample. Or, we read

$$\sigma^2_{y_s}=y_s\left(1-\frac{y_s}{m}\right) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{(i)},$$

where y_s is now taken as the frequency of the s^{th} group in the sample.

PROBLEM II. *To find the correlation between deviations in y_s and $y_{s'}$, or between deviations in the frequencies of the s^{th} and s'^{th} groups.*

Let $\delta y_s =$ deviation from y_s the most probable value in the s^{th} group, then since

$$y_1+y_2+y_3+\ldots+\ y_s+\ldots+\ y_{s'}+\ldots+y_n\ =m,$$
$$\delta y_1+\delta y_2+\delta y_3+\ldots+\delta y_s+\ldots+\delta y_{s'}+\ldots+\delta y_n=0.$$

Now if our sample has given δy_s too many in y_s, it is proper to suppose that this error will be distributed among the other groups in the proportion of their relative frequencies*. In other words we should have

$$\delta y_s'=-\ \delta y_s \times \frac{y_{s'}}{m-y_s}.$$

Thus:

$$\delta y_s'\,\delta y_s=-\frac{(\delta y_s)^2}{m}\,\frac{y_{s'}}{1-y_s/m}.$$

Summing for all samplings

$$\sigma_{y_{s'}}\sigma_{y_s}r_{y_s y_{s'}}=-\frac{\sigma^2_{y_s}}{m}\,\frac{y_{s'}}{1-y_s/m}=-\frac{y_s y'_{s'}}{m} \text{ by (i).}$$

Hence

$$\sigma_{y_s}\sigma_{y_{s'}}r_{y_s y_{s'}}=-\frac{y_s y'_{s'}}{m} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{(ii)}.$$

PROBLEM III. *To find the standard deviation σ_h of the mean h of a system of observations.*

Measured from a fixed point of reference, we have:

$$h=\frac{S(xy)}{S(y)}=\frac{S(xy)}{m},$$

where y is the frequency of individuals of size x.

* This of course assumes that the error is merely due to random sampling, and not to defective measurement or classificatory judgment. In such cases the error in δy_s might, for example, be especially drawn from the "adjacent" classes y_{s-1} and y_{s+1}.

Therefore

$$m\delta h = S(x\delta y),$$
$$m^2(\delta h)^2 = S(x_s^2\,\delta y_s^2) + 2S'(x_s x_{s'}\,\delta y_s\,\delta y_{s'}),$$

where S' is a sum for all values of s and s' for which s is not equal to s'. This gives dividing by the number of random samplings after summing for all such samples:

$$m^2\sigma_h^2 = S(x_s^2\sigma^2_{y_s}) - 2S'(x_s x_{s'}\sigma_{y_s}\sigma_{y_{s'}}r_{y_s y_{s'}}),$$

or, using (i) and (ii)

$$m^2\sigma_h^2 = S(x_s^2 y_s) - S\left(x_s^2\frac{y_s^2}{m}\right) - 2S'\left(x_s x_{s'}\frac{y_s y_{s'}}{m}\right)$$
$$= m\mu_2' - m\frac{S(x_s y_s)}{m}\times\frac{S(x_{s'}y_{s'})}{m}$$
$$= m(\mu_2' - h^2),$$

where $m\mu_2'$ is the second moment about the fixed point. But $\mu_2' - h^2 = \sigma^2$ = square of standard deviation of sample. Hence:

$$\sigma_h = \sigma/\sqrt{m} \quad \text{.....(iii).}$$

PROBLEM IV. *To find the standard deviation of the q^{th} moment $= m\mu_q'$ of the sample* **about a fixed point.**

$$m\mu_q' = S(x_s^q y_s).$$

Therefore

$$m\delta\mu'_q = S(x_s^q\,\delta y_s),$$

and

$$m^2\sigma^2_{\mu'_q} = S(x_s^{2q}\sigma^2_{y_s}) + 2S'(x_s^q x_{s'}^q \sigma_{y_s}\sigma_{y_{s'}}r_{y_s y_{s'}})$$

as before. Using (i), and (ii), we have

$$m^2\sigma^2_{\mu'_q} = S(x_s^{2q}y_s) - \frac{S(x_s^{2q}y_s^2)}{m} - \frac{2S'(x_s^q x_{s'}^q y_s y_{s'})}{m}$$
$$= m\mu'_{2q} - m\mu_q'\times\mu_q',$$

or

$$\sigma_{\mu'_q} = \frac{\sqrt{\mu'_{2q} - \mu'^2_q}}{\sqrt{m}} \quad \text{..... (iv).}$$

PROBLEM V. *To find the correlation of errors of the q^{th} and q'^{th} moments,* **both moments being taken about the same fixed point.**

As in Problem IV.:

$$m\delta\mu'_q = S(x_s^q\,\delta y_s),$$
$$m\delta\mu'_{q'} = S(x_s^{q'}\delta y_s).$$

Multiplying these together:

$$m^2\delta\mu'_q\delta\mu'_{q'} = S(x_s^{q+q'}\delta y_s^2) + S'\{(x_s^q x_{s'}^{q'} + x_{s'}^q x_s^{q'})\,\delta y_s\delta y_{s'}\},$$

or, using the definitions of correlation and standard deviation:

$$m^2\sigma_{\mu'_q}\sigma_{\mu'_{q'}}r_{\mu'_q\mu'_{q'}} = S(x_s^{q+q'}\sigma^2_{y_s}) + S'\{(x_s^q x_{s'}^{q'} + x_{s'}^q x_s^{q'})\,\sigma_{y_s}\sigma_{y_{s'}}r_{y_s y_{s'}}\}.$$

Hence by (i) and (ii)

$$m^2\sigma_{\mu'_q}\sigma_{\mu'_{q'}}r_{\mu'_q\mu'_{q'}} = m\mu'_{q+q'} - m\mu'_q\mu'_{q'}.$$

Thus

$$\sigma_{\mu'_q}\sigma_{\mu'_{q'}}r_{\mu'_q\mu'_{q'}} = \frac{\mu'_{q+q'} - \mu'_q\mu'_{q'}}{m} \quad \text{..... (v),}$$

(iv) and (v) thus give the standard deviation of errors in any moment and the correlation in errors between two moments, when the moments are taken *about a fixed point.* We now require to find

the standard deviation in errors in any moment, and the correlation of errors in moments, when these moments are taken, not about a fixed point, but about the mean, which is a point varying with the errors of random sampling.

PROBLEM VI. *To find the correlation between an error in the mean and an error in the q^{th} moment both determined from a fixed point.*

This is given at once by (v) since $h=\mu_1'$. We have only to put $q'=1$, and we have

$$\sigma_{\mu'_q}\sigma_h r_{h\mu'_q}=\frac{\mu'_{q+1}-h\mu'_q}{m} \quad \text{.....(vi).}$$

Now it may be noted once and for all that *after* these expressions like (iv), (v) and (vi) have been found we can calculate the right-hand side taking for our fixed point any origin we please, i.e. we can take the point which actually coincides with the mean in the sample, i.e. write $h=0$, and $\mu'_q=\mu_q$, where μ_q is the moment about the observed mean.

PROBLEM VII. *To find the standard deviation for errors in the q^{th} moment μ_q* **taken about the mean.**

We have:

$$\begin{aligned} m\mu_q &= S\{(x_s-h)^q y_s\} \\ &= m\left(\mu'_q - qh\mu'_{q-1}+\frac{q(q-1)}{1.2}h^2\mu'_{q-2}+\ldots\right). \end{aligned}$$

Or:

$$\mu_q=\mu'_q-qh\mu'_{q-1}+h^2\chi,$$

where χ is a function of q, h and μ'_{q-2}, μ'_{q-3}, etc.

Hence:

$$\delta\mu_q=\delta\mu'_q-qh\delta\mu'_{q-1}-\delta h\,(q\mu'_{q-1}+2h\chi)+\text{terms in } h^2 \text{ and higher powers.}$$

Thus if we are going to put $h=0$ finally or measure our moments from a fixed point, which coincides with the actual position of the mean in the sample, we may write:

$$\delta\mu_q=\delta\mu'_q-q\,\delta h\,\mu'_{q-1}+\text{terms which vanish with } h.$$

Thus:

$$\delta\mu_q{}^2=\delta\mu'_q{}^2+q^2\delta h^2\mu'^2_{q-1}-2q\mu'_{q-1}\delta h\,\delta\mu'_q+\text{terms vanishing with } h.$$

Or:

$$\sigma^2_{\mu_q}=\sigma^2_{\mu'_q}+q^2\sigma_h{}^2\mu'^2_{q-1}-2q\mu'_{q-1}\sigma_h\sigma_{\mu'_q}r_{h\mu'_q}+\text{terms in } h,$$

and using (iv), (iii) and (vi):

$$\sigma^2_{\mu_q}=\frac{\mu'_{2q}-\mu'^2_q+q^2\sigma^2\mu'^2_{q-1}-2q\mu'_{q-1}\mu'_{q+1}+\text{terms in } h}{m}.$$

Put $h=0$, and $\mu'_i=\mu_i$, we have:

$$\sigma_{\mu_q}=\sqrt{\frac{\mu_{2q}-\mu^2_q-2q\mu_{q+1}\mu_{q-1}+q^2\sigma^2\mu^2_{q-1}}{m}} \quad \text{..... (vii).}$$

Illustrations.

(i) Put $q=2$, and remember that $\mu_1=0$.

$$\text{Probable error of } \mu_2=\cdot67449\sqrt{\frac{\mu_4-\mu_2{}^2}{m}}.$$

For example, in the case of a normal curve this $=\cdot67449\sqrt{\frac{2}{m}}\mu_2$, since $\mu_4=3\mu_2{}^2$.

Further we have, since $\sigma=\sqrt{\mu_2}$, for the normal curve

$$\text{Probable error of } \sigma=\cdot67449\sqrt{\frac{1}{2m}}\sigma.$$

(ii) Put $q=3$. $\quad$ Probable error of $\mu_3=\cdot67449\sqrt{\frac{\mu_6-\mu_3{}^2-6\mu_4\mu_2+9\mu_2{}^3}{m}}$.

For example, in the case of a normal curve $\mu_4=3\mu_2^2$, $\mu_6=15\mu_2^3$, and $\mu_3=0$, therefore

$$\text{Probable error of } \mu_3 = \cdot 67449 \sqrt{\frac{15\sigma^6-18\sigma^6+9\sigma^6}{m}} = \cdot 67449 \sqrt{\frac{6}{m}}\sigma^3,$$

and a curve should not by this criterion alone be assumed not to be normal unless the observed μ_3 is at least two or three times as large as

$$\cdot 67449 \sqrt{\frac{6}{m}}\sigma^3.$$

(iii) Put $q=4$.

$$\text{Probable error of } \mu_4 = \cdot 67449 \sqrt{\frac{\mu_8-\mu_4^2-8\mu_5\mu_3+16\mu_2\mu_3^2}{m}}.$$

For the normal curve since $\mu_3=0$, this reduces to

$$\cdot 67449 \sqrt{\frac{\mu_8-\mu_4^2}{m}} = \cdot 67449 \sqrt{\frac{96}{m}}\sigma^4,$$

the former value being exactly the same expression as holds for moments about a fixed point.

PROBLEM VIII. *To find the correlation in errors in two moments* **both measured from the mean.**

As in the last problem:

$$\delta\mu_q = \delta\mu'_q - q\delta h\mu'_{q-1} + \text{terms in } h,$$
$$\delta\mu_{q'} = \delta\mu'_{q'} - q'\delta h\mu'_{q'-1} + \text{terms in } h.$$

Hence:

$$\delta\mu_q\,\delta\mu_{q'} = \delta\mu'_q\delta\mu'_{q'} + qq'(\delta h)^2\mu'_{q-1}\mu'_{q'-1} - q'\delta h\,\delta\mu'_q\mu'_{q'-1} - q\,\delta h\,\delta\mu'_{q'}\mu'_{q-1} + \text{terms in } h.$$

Thus:

$$\sigma_{\mu_q}\sigma_{\mu_{q'}}r_{\mu_q\mu_{q'}} = \sigma_{\mu'_q}\sigma_{\mu'_{q'}}r_{\mu'_q\mu'_{q'}} + qq'\sigma_h^2\mu'_{q-1}\mu'_{q'-1} - q'\sigma_h\sigma_{\mu'_q}r_{h\mu'_q}\mu'_{q'-1} - q\sigma_h\sigma_{\mu'_{q'}}r_{h\mu'_{q'}}\mu'_{q'-1} + \text{terms in } h.$$

Using (v) and (vi) we find:

$$\sigma_{\mu_q}\sigma_{\mu_{q'}}r_{\mu_q\mu_{q'}} = \frac{\mu'_{q+q'} - \mu'_q\mu'_{q'} + qq'\sigma^2\mu'_{q-1}\mu'_{q'-1} - q'\mu'_{q+1}\mu'_{q'-1} - q\mu'_{q-1}\mu'_{q'+1} + \text{terms in } h}{m}.$$

Putting $h=0$, $\mu_i'=\mu_i$, we find:

$$\sigma_{\mu_q}\sigma_{\mu_{q'}}r_{\mu_q\mu_{q'}} = \frac{\mu_{q+q'} - \mu_q\mu_{q'} + qq'\sigma^2\mu_{q-1}\mu_{q'-1} - q'\mu_{q+1}\mu_{q'-1} - q\mu_{q-1}\mu_{q'+1}}{m} \quad \ldots\ldots\ldots \text{(viii)}.$$

Illustrations.

(i) Suppose $q=2$, $q'=3$, then remembering $\mu_1=0$,

$$\sigma_{\mu_2}\sigma_{\mu_3}r_{\mu_2\mu_3} = \frac{\mu_5-\mu_2\mu_3-3\mu_3\mu_2}{m} = \frac{\mu_5-4\mu_2\mu_3}{m}.$$

(ii) Suppose $q=2$, $q'=4$,

$$\sigma_{\mu_2}\sigma_{\mu_4}r_{\mu_2\mu_4} = \frac{\mu_6-\mu_2\mu_4-4\mu_3^2}{m}.$$

(iii) Suppose $q=3$, $q'=4$,

$$\sigma_{\mu_3}\sigma_{\mu_4}r_{\mu_3\mu_4} = \frac{\mu_7-\mu_3\mu_4+12\mu_2^2\mu_3-4\mu_4\mu_3-3\mu_2\mu_5}{m}$$
$$= \frac{\mu_7-5\mu_3\mu_4+12\mu_2^2\mu_3-3\mu_2\mu_5}{m}.$$

Lastly, to find certain probable errors we require:

PROBLEM IX. *To find the correlation between errors in the q^{th} moment about the mean and the q'^{th} moment about a fixed point, in terms of these moments.*

In order to work out this problem we take a preliminary proposition:

To find the correlation between an error in the group y_s and an error in the moment $\mu'_{q'}$ about a fixed point.

We have:

$$m\mu'_{q'} = S(x_s^{q'} y_s),$$

therefore:

$$m\delta\mu'_{q'}\delta y_s = x_s^{q'}(\delta y_s)^2 + S'(x_{s'}^{q'}\delta y_s \delta y_{s'}),$$

$$m\sigma_{\mu'_{q'}}\sigma_{y_s} r_{\mu'_{q'} y_s} = x_s^{q'} y_s \left(1 - \frac{y_s}{m}\right) - \frac{S'(x_{s'}^{q'} y_s y_{s'})}{m}$$

$$= y_s\left(x_s^{q'} - \frac{S(x_s^{q'} y_s)}{m}\right),$$

or:

$$\sigma_{\mu'_{q'}}\sigma_{y_s} r_{\mu'_{q'} y_s} = \frac{y_s(x_s^{q'} - \mu'_{q'})}{m} \quad \text{..... (ix).}$$

This is the correlation between an error in y_s and one in the q'^{th} moment about a fixed point.

To find the correlation between an error in y_s and one in the q^{th} moment about the mean, we have as before:

$$\delta\mu_q = \delta\mu'_q - q\delta h\mu'_{q-1} + \text{terms in } h,$$

$$\delta\mu_q \delta y_s = \delta\mu'_q dy_s - q\delta h\,\delta y_s \mu'_{q-1} + \text{terms in } h,$$

$$\sigma_{\mu_q}\sigma_{y_s} r_{\mu_q y_s} = \sigma_{\mu'_q}\sigma_{y_s} r_{\mu'_q y_s} - q\sigma_h \sigma_{y_s} r_{h y_s}\mu'_{q-1} + \text{terms in } h,$$

$$= \frac{y_s(x_s^q - \mu'_q)}{m} - \frac{q y_s (x_s - h)}{m}\mu'_{q-1} + \text{ terms in } h,$$

since $h = \mu_1'$ and we can use (ix). Hence putting $h=0$, we have

$$\sigma_{\mu_q}\sigma_{y_s} r_{\mu_q y_s} = \frac{y_s(x_s^q - \mu_q - q x_s \mu_{q-1})}{m} \quad \text{..... (x),}$$

x being here measured from the mean.

Illustrations.

(i) To find the correlation between an error in any single group and an error in the mean.

We have from (ix) when $q'=1$, $h=\mu_1'$,

$$\sigma_h \sigma_{y_s} r_{h y_s} = \frac{y_s(x_s - h)}{m}$$

$$= \frac{y_s x_s}{m}, \text{ if } x_s \text{ be measured from mean.}$$

(ii) To find the correlation between the error in the standard deviation and an error in any single group.

We have from (x) if $q=2$,

$$\sigma_{\mu_2}\sigma_{y_s} r_{\mu_2 y_s} = \frac{y_s(x_s^2 - \mu_2)}{m}.$$

But $\mu_2 = \sigma^2$

$$\delta\mu_2 = 2\sigma\delta\sigma,$$

therefore:

$$\delta\mu_2 \delta y_s = 2\sigma\delta y_s \delta\sigma,$$

and

$$\sigma_{\mu_2}\sigma_{y_s} r_{\mu_2 y_s} = 2\sigma\sigma_{y_s}\sigma_\sigma r_{y_s \sigma}.$$

Further: $$\delta\mu_2^2 = 4\sigma^2\delta\sigma^2,$$

$$\sigma^2_{\mu_2} = 4\sigma^2\sigma^2_\sigma,$$

whence we see: $$r_{\mu_2 y_s} = r_{y_s\sigma}.$$

Thus we find: $$\sigma_{\mu_2}\sigma_{y_s} r_{\sigma y_s} = -\frac{y_s(\sigma^2 - x_s^2)}{m}.$$

Thus if an error be made in the frequency of a group with character less than σ, the error in the standard deviation will be negatively correlated with it. If the error be in a frequency group with character greater than σ, the error in σ will be positively correlated with the error in the group.

We can now return to our original problem. We have:

$$m\delta\mu'_{q'} = S(x_s^{q'}\delta y_s),$$

$$\delta\mu_q = \delta\mu'_q - q\delta h\,\mu'_{q-1} + \text{terms in } h,$$

$$m\delta\mu'_{q'}\delta\mu_q = S(x_s^{q'}\delta y_s\delta\mu'_q) - q\mu'_{q-1}S(x_s^{q'}\delta y_s\delta h) + \text{terms in } h,$$

$$\sigma_{\mu'_{q'}}\sigma_{\mu_q} r_{\mu'_{q'}\mu_q} = \frac{S\{x_s^{q'} y_s (x_s^q - \mu'_q)\}}{m^2} - q\mu'_{q-1}\frac{S\{x_s^{q'} y_s (x_s - h)\}}{m^2} + \text{terms in } h,$$

$$= \frac{\mu'_{q+q'} - \mu'_{q'}\mu'_q}{m} - \frac{q\mu'_{q-1}\mu'_{q'+1}}{m} + \text{terms in } h.$$

Whence putting $h=0$, we have for the correlation of errors in the two kinds of moments, i.e. those measured from a fixed point and those measured from the mean:

$$\sigma_{\mu'_{q'}}\sigma_{\mu_q} r_{\mu'_{q'}\mu_q} = \frac{\mu_{q+q'} - \mu_{q'}\mu_q - q\mu_{q-1}\mu_{q'+1}}{m} \quad \text{..... (xi).}$$

The chief use of this formula is to find the correlation of errors in the mean and in the moments about the mean. For this purpose put $q'=1$, i.e. $\mu'_{q'}=h$, and we have since $\mu_1=0$, on right-hand side:

$$\sigma_h\sigma_{\mu_q} r_{h\mu_q} = \frac{\mu_{q+1} - q\mu_{q-1}\mu_2}{m} \quad \text{..... (xii).}$$

Illustrations.

(i) To find the correlation in error between the mean and the standard deviation.

All we need to do is to put $q=2$, then:

$$\sigma_h\sigma_{\mu_2} r_{h\mu_2} = \mu_3/m.$$

But $r_{h\mu_q} = r_{h\sigma}$, therefore

$$\sigma_h\sigma_{\mu_2} r_{h\sigma} = \mu_3/m \quad \text{..... (xiii).}$$

Hence if a random sample be taken which is more variable than the general population, the probability is that the mean of the sample will be higher than the mean of the general population if the third moment be positive, and lower if it be negative. Thus we cannot by random sampling change the variability without changing the type or the type without changing the variability. The only exception occurs when $\mu_3=0$, for example in the normal curve. In that case errors in the mean are independent of errors in the variability.

(ii) To find the correlation in error between the mean and the third moment.

Put $q=3$ in (xii), we have

$$\sigma_h\sigma_{\mu_3} r_{h\mu_3} = \frac{\mu_4 - 3\mu_2^2}{m}.$$

This vanishes again in the case of the normal curve. It may be shewn that the correlation between the mean and all the moments vanishes for normal systems and normal systems only.

GENERAL PROBLEM. *To find the probable error of any constant c_i of a frequency distribution and the correlation of any two constants c_i and $c_{i'}$.*

Any constant will be a function of the mean h and the moments $\mu_2, \mu_3, \mu_4, \ldots \mu_q \ldots$ about the mean. Hence:

$$c_i = \phi(h,\ \mu_2,\ \mu_3,\ \mu_4 \ldots \mu_q \ldots),$$

and if the errors be small as compared with the quantities in which they occur we can write

$$\delta c_i = \phi_h \delta h + \phi_{\mu_2} \delta\mu_2 + \phi_{\mu_3} \delta\mu_3 + \ldots\ldots$$

where ϕ_h, $\phi_{\mu_2}, \ldots$ are the differentials of the known function ϕ with regard to the subscript quantities. Hence their numerical values are known and we may write, if λ denotes a known numerical quantity:

$$\delta c_i = \lambda_1 \delta h + \lambda_2 \delta\mu_2 + \lambda_3 \delta\mu_3 + \ldots\ldots .$$

Square, sum and divide by the number of cases and we have:

$$\begin{aligned}\sigma^2_{c_i} &= \lambda_1{}^2\sigma_h{}^2 + \lambda_2{}^2\sigma^2_{\mu_2} + \lambda_3{}^2\mu_3{}^2 + \ldots\ldots \\ &\quad + 2\lambda_1\lambda_2\sigma_h\sigma_{\mu_2} r_{h\mu_2} + 2\lambda_1\lambda_3\sigma_h\sigma_{\mu_3} r_{h\mu_2} + \ldots\ldots \\ &\quad + 2\lambda_2\lambda_3\sigma_{\mu_2}\sigma_{\mu_3} r_{\mu_2\mu_3} + \ldots\ldots \\ &= \lambda_1{}^2\sigma_h{}^2 + S(\lambda_q{}^2\sigma^2_{\mu_q}) \\ &\quad + 2\lambda_1\sigma_h S(\lambda_q \sigma_{\mu_q} r_{h\mu_q}) \\ &\quad + 2S'(\lambda_q\lambda_{q'}\sigma_{\mu_q}\sigma_{\mu_{q'}} r_{\mu_q\mu_{q'}}) \ldots\ldots\ldots\

(*a*) Normal Curve: $$y=y_0 e^{-\frac{x^2}{2\sigma^2}},$$

$$\mu_{2n}=(2n-1)\,\sigma^2\mu_{2n-2}.$$

(*b*) Curve of Type:

$$y=y_0\left(1+\frac{x}{a}\right)^p e^{-\gamma x},$$

Origin at mode and $p=a\gamma$,

$$\mu_{n+1}=\frac{n}{\gamma}\mu_n+\frac{n(p+1)}{\gamma^2}\mu_{n-1}.$$

(*c*) Curve of Type:

$$y=y_0\left(1+\frac{x}{a_1}\right)^{m_1}\left(1-\frac{x}{a_2}\right)^{m_2},$$

Origin at mode and $b=a_1+a_2$, $r=m_1+m_2+2$,

$$\mu_{n+1}=\frac{nb(m_2-m_1)}{r(r+n)}\mu_n+\frac{nb^2(m_1+1)(m_2+1)}{r^2(r+n)}\mu_{n-1}.$$

(*d*) Curve of Type:

$$y=y_0\left\{1+\frac{x^2}{a^2}\right\}^{-\frac{r+2}{2}} e^{-\nu\tan^{-1}\frac{x}{a}},$$

Origin at $-a\nu/r$ from mean and $\tan\phi=\nu/r$,

$$\mu_{n+1}=\frac{n}{r-n}\left(\frac{a^2\mu_{n-1}}{\cos^2\phi}-2a\tan\phi\,\mu_n\right).$$

(*e*) The general formula of reduction for

$$\frac{1}{y}\frac{dy}{dx}=\frac{a_0+a_1x}{c_0+c_1x+c_2x^2+c_3x^3+c_4x^4+\ldots},$$

Origin at the mean is,

$$nc_0\mu_{n-1}+\{(n+1)c_1+a_0\}\mu_n+\{(n+2)c_2+a_1\}\mu_{n+1}$$
$$+(n+3)c_3\mu_{n+2}+(n+4)c_4\mu_{n+3}+\ldots=0.$$

As a practical illustration of the use of these formulae the reader is referred to a criticism of Professor von Török's recent craniological work appearing in this part of *Biometrika*.

THIRD REPORT ON HYBRIDS BETWEEN WALTZING MICE AND ALBINO RACES.

ON THE RESULT OF CROSSING JAPANESE WALTZING MICE WITH "EXTRACTED" RECESSIVE ALBINOS.

By A. D. DARBISHIRE, Balliol College, Oxford.

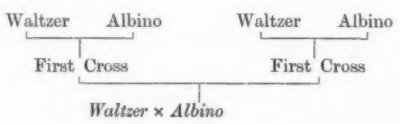
As is well known to those familiar with this question, it is an essential part of the Mendelian hypothesis that the (so-called "extracted") recessive individual which is produced by pairing two first crosses, is in every respect similar to the original pure recessive. It forms, in fact, the foundation on which the doctrine of the purity of the germ-cells rests. To put the matter more explicitly, the extracted recessive is identical with the original pure recessive and is not affected by its unusual ancestry in any way.

It is the object of the present report to describe three different kinds of crosses which show that the character of the offspring of extracted albinos is determined by (or at any rate correlated with) the ancestry of the albino parent.

I have crossed pure-bred waltzing mice, not with pure-bred albinos, but with extracted recessive albinos: now, the offspring thus obtained are either correlated with their grandparents (i.e. the hybrid parents of the albino), or, they are not. That is to say the character of the grandparent either has some effect on the character of the grandchildren or it has not.

I hope the following cases will show that it has.

1. Pure-bred waltzing mice were crossed with albinos produced by pairing two first crosses together. Thus:



Three families have been produced from such a cross. The parents of the albinos used had always wild-colour in the coat, and the offspring of these unions had invariably the same colour. The results are given in Table I., below.

TABLE I*.

Catalogue Number of Cross	Character of Offspring	Character of Grandparents on albino side
130	2*c*, 2*c*	♀ 2*c* × ♂ 3*c*
148	3*c*, 3*c*, 3*c*, 3*c*, 3*c*, 3*c*	♀ 3*c* × ♂ 3*c*
150	2*c*, 2*c*, 2*c*, 2*c*, 3*c*	♀ 3*c* × ♂ 3*c*

2. Pure-bred waltzing mice have also been crossed with albinos produced by crossing a hybrid with an albino. Thus:

Waltzer Albino

First Cross Albino

Waltzer × *Albino*

And the measure of the correlation which exists with regard to colour between offspring thus produced and the hybrid grandparent is shown in Table II.

TABLE II.

Colour of Grandchild.

Hybrid Grandparent.	Yellow (*a*)	Wild (*c* or *d*)	Totals
(*a*)	8	4	12
(*c* or *d*)	1	67	68
Totals	9	71	80

Working out this table by the method for dealing with quantitatively indeterminate characters, we find, using the notation of *Phil. Trans.* A., Vol. 195, p. 6,

$$h = 1{\cdot}21344, \quad k = 1{\cdot}03643,$$

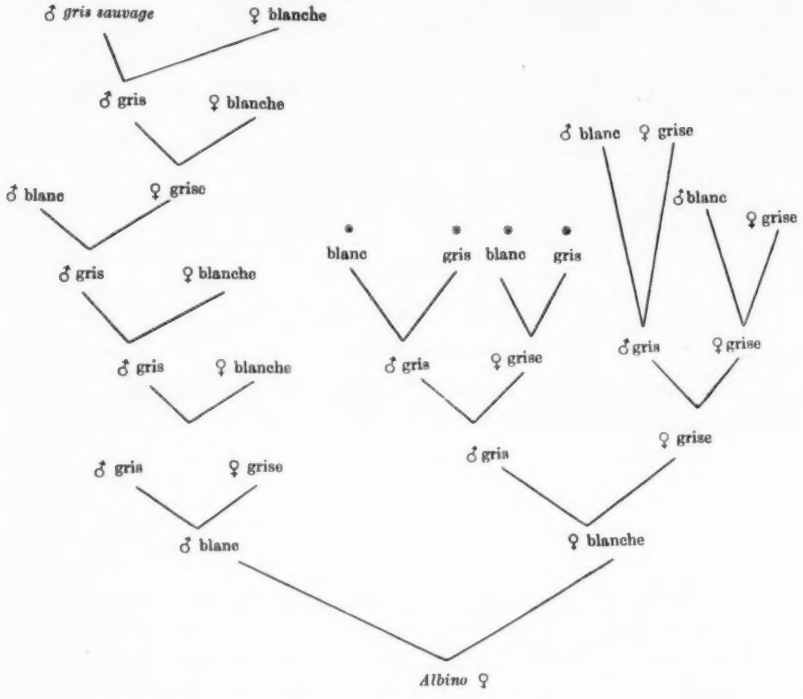
with an equation of many terms having the solution

$$r = {\cdot}951.$$

This correlation between grandparent and grandchild with regard to a "dominant character" transmitted through the recessive parent seems to dispose entirely of any theory which involves the gametic purity of the recessive parent.

* The notation being the same as in the last Report. *Biometrika*, Vol. II. p. 165.

3. I have made one cross between a pure-bred waltzing mouse ♂ and an albino ♀ extracted from crosses between albinos and house-mice. The albino was given me by Professor Cuénot: and I wish to take this opportunity for thanking him for his courtesy and kindness to me. The ancestry of the albino is, in Professor Cuénot's words, as follows:



That is to say the amount of wild-colour in the ancestry is very great: the seven offspring produced by this mouse crossed with a waltzer were all completely wild-coloured.

4. So far we have been considering the colour of those portions of the coat which were not white.

The correlation between the amount of white in the coats of hybrid grandparent, parent of albino, and its grandchildren is given in Table III.

* Which parent was white and which grey is not known.

TABLE III.

Amount of Whiteness *.

Grandchild.

Grandparent.		*2—3*	*4—6*	Totals
	2—3	23	15	38
	4—6	13	29	42
	Totals	36	44	80

5. A last important difference, upon which I will not at present comment, lies in this. The cross between the ordinary albino and the pure waltzer has so far invariably given dark-eyed young, but out of the eighty young already produced by crossing extracted albinos with pure waltzers five have pink eyes.

Doubtless different people will interpret these phenomena in different ways: but the subject of the present paper is not a question of interpretation but of fact: and I have confined myself to the mere statement of the fact until a larger number of cases justify an attempt at interpretation.

Postscript. Added June 4th. The foregoing account treats only of the offspring of extracted recessives. A mouse of the same generation as the latter, a waltzer with pink eyes and a yellow and white coat ($G'G'$ of Mr Bateson's notation,—the form which Castle asserts to be the extracted dominant) has served four pure-bred albino does; three of which have families old enough for description. In the notation of my previous reports they may be described as follows:

No. of Cross	Offspring
145	5*b*, 5*b*, 6*b*, 5*b*, 6*b*, 5*c*, and 1 albino
146	5*a*, 5*c*, 5*c*, 4*c*, and 4 albinos
156	2*c*, 5*c*, and 3 albinos

This mouse is clearly not a pure dominant, because it produces albinos; it is not a dominant hybrid because it has pink eyes; and it cannot be a recessive because when paired with an albino it produces some black-eyed forms.

* Scale of whiteness is that of the Second Report. I find $h = \cdot1257$, $k = \cdot0627$, and the equation for r

$$\cdot04204r^7 + \cdot00243r^6 + \cdot07207r^5 + \cdot00294r^4 + \cdot16339r^3 + \cdot00394r^2 + r - \cdot46798 = 0.$$

The solution of which is $r = \cdot451$.

Thus in this case as in the previous one we see the ancestry of recessive individuals is of importance, for a very sensible correlation exists between the offspring and the grandparent with which the offspring are connected through their recessive parent.

Mr BATESON'S REVISIONS OF MENDEL'S THEORY OF HEREDITY.

By W. F. R. WELDON, F.R.S.

The results which Mr Darbishire has so far obtained by crossing pink-eyed piebald waltzing mice with normal pink-eyed albinos have been recorded in the last two numbers of *Biometrika*. In *Nature* of March 19 and April 23 Mr Bateson has stated his belief that the inheritance of eye-colour in these mice is "strictly Mendelian," and he has published a Mendelian formula which implies his belief that the inheritance of coat colour is Mendelian also. In order to fully understand Mr Bateson's treatment it is necessary to realise not only Mendel's own doctrines, but the various modifications of these which Mr Bateson has from time to time propounded. Only after such preliminary survey can we discuss the bearing of the facts established by Mr Darbishire in his work on mice.

Mendel's Theory of Hybrids.

Mendel made two general statements, describing the results which he says he invariably obtained in his experiments with cross-bred peas; the first is what is often called his *Law of Dominance*, and describes the manner in which characters are transmitted from the pure-bred parents to the hybrid resulting from their union; the second is his *Law of Segregation* (Spaltungsgesetz, Loi de Disjonction) and describes the characters of the subsequent generations, descended from the hybrids originally produced; to account for the phenomena described by his Law of Segregation, he puts forward a theory of the constitution of the germ-cells, both in pure-bred individuals and in hybrids.

Mendel was the first to systematically analyse the differential characters of a race or species into a series of unit-characters, each of which might, under suitable conditions, be inherited independently of the others; in this he anticipated the essential features of the view afterwards developed (without knowledge of Mendel's work) by de Vries. Mendel further anticipated speculations of de Vries and Weismann by attributing the inheritance of each unit-character to the

presence of a particular unit element in the germ-cell; and this conception of the "mechanism" of inheritance enabled him to formulate his hypothesis of the constitution of the germ-cells in the class of hybrids which he studied. He believed that if two races differ in a particular unit-character, which had the condition A in one race, the condition a in another, the gametes of the two races will differ; in the one race, each gamete produced will contain an element A, each gamete of the other race containing an element a. In the normal process of reproduction by individuals of like race, male and female gametes of like constitution meet, and their corresponding elements unite; so that the complete zygote from which a pure-bred individual of our first race arises, contains an element AA, derived in part from each parent; when an individual of one race is paired with an individual of the other race, the hybrid zygote contains an element Aa. Now in cases such as those Mendel observed, he supposes that when the hybrid, resulting from a zygote Aa forms germ-cells for itself, each of its germ-cells contains *either* an element A only, *or* an element a only; and germ-cells of each kind are formed in equal numbers, half of each kind being male, and half female. When such hybrids are paired together, three kinds of union are possible; gametes of like constitution may unite, giving rise to zygotes of constitution AA or aa, or gametes of unlike kind may unite, and give rise to zygotes of constitution Aa. As the union is supposed to occur by chance, zygotes of constitution Aa will occur, in any large series of cases, twice as frequently as zygotes AA or aa. In all his discussions of such hybrids Mendel assumes that the Law of Dominance will hold, as he tells us it always held in the cases he examined; he therefore assumes that the first formed hybrid, though containing elements Aa, will present the appearance of an individual belonging to the race in which the unit character has the "dominant" condition, say A; the offspring of such hybrids will externally be of two kinds; one quarter resembling the race a and capable of transmitting only the characters proper to that race, three quarters resembling the race A; but of these three quarters with dominant appearance, one will contain only elements A and will, therefore, be capable of transmitting only the characters of race A, while the other two are of composition Aa, and behave like their hybrid parents if allowed to breed.

If the two pure-bred parents differ in more than one unit character, all the elements which represent the various differential characters are separated in the hybrid body during gamete-formation, and each behaves independently of the others; thus an individual of pure race distinguished by two unit characters A and B, when paired with an individual of another pure race with characters a and b, will give rise to a hybrid of constitution $Aa + Bb$; and when this hybrid forms its gametes, separate elements A, a, B, b, will be formed in equal numbers and united in the gametes in each of the four possible ways with equal frequency; so that there will be four equally numerous sets of gametes, of constitution $(A + B)$, $(A + b)$, $(a + B)$, and $(a + b)$. A similar process of resolution and reconstruction is supposed to occur in more complex cases.

Mendel considered that the unit character could only be determined by experiment; on the one hand groups of apparently distinct characters might be inherited as one unit (for example seed-coat colour and flower colour in certain peas) while on the other hand an apparently single character, such as the colour of some flowers, might be due to the simultaneous presence of several unit characters, each capable of being inherited separately from the others.

Mr Bateson's Revisions of Mendel.*

1. *The nature of the gametes in hybrids.*—Mendel says that the gametes, produced by a hybrid zygote of constitution Aa, are not themselves hybrid, but are of two kinds, both equally numerous; one kind contains only elements A, the other containing only elements a. Now when similar gametes, produced in this way, unite to form a zygote, what will happen? The individuals will behave like pure-bred individuals of the race represented by their gametes. This is all that Mendel ever asserts of them; when he says that their characters remain constant, it is clear that he means a constancy of the same order as that observed within the limits of a pure-bred species because he treats the species as themselves constant, and so neglects individual variation within the limits of a single race. Mr Bateson however, alone among modern naturalists, roundly declares that "the pure dominant and pure recessive members of each generation are not merely like but identical with the pure parents" (II. p. 12); so that one of the effects attributed by him to cross-breeding is the disappearance of those differences which normally exist between members of the same species. He asserts that by cross-breeding a group of individuals may be produced, including one ancestor and some of its grandchildren, great grandchildren and more remote posterity ("members *of each generation*") which are "not merely like but identical with" each other. This statement is supported by no scrap of evidence; it is flatly contradicted by experiments which Mr Bateson himself adduces as "following Mendel's law with considerable accuracy" (e.g., the experiments with *Datura*, (II. pp. 21—32)); nevertheless, it is made the basis of the imposing dogma that any attempt to express the characters of the hybrids described in terms of all their various ancestors is henceforth futile; the suggestion that the discrepancies between Mendel's own results and those of subsequent observers who have endeavoured to repeat his observations may be accounted for by differences in the ancestry of the peas used is regarded by Mr Bateson as an attempt to mask a difficulty one dare not face (I. p. 200).

2. *The essentials of Mendel's theory.*—Having made the striking addition to Mendel's statements, described in the last paragraph, Mr Bateson proceeds to

* The statements here discussed are chiefly contained in the following works, which will be referred to as I. and II.:

I.—*Mendel's Principles of Heredity:* a Defence, by W. Bateson. 8vo. Cambridge, 1902.

II.—*Reports to the Evolution Committee of the Royal Society:* I. Experiments undertaken by W. Bateson and Miss E. R. Saunders. Roy. Soc., 1902.

separate what he considers essential in them from what is not. The phenomenon of dominance, though always observed by Mendel, is not essential; and in asserting this proposition Mr Bateson does not hesitate to accuse his master of something very like a gross breach of good faith. Mendel's description of the result obtained by crossing peas is translated by Mr Bateson in these words: "In the case of each "of the seven crosses the hybrid character resembles that of one of the parental "forms so closely that the other either escapes observation completely or cannot "be detected with certainty" (I. p. 49). This is a clear and unequivocal statement of an observed experimental result, that in each of seven crosses dominance was observed. No honest observer could have formulated this statement if he had observed any large number of exceptions, and it seems to me that no one can read Mendel's paper without believing him to be absolutely honest; yet Mr Bateson thinks it fair to suppose that the behaviour of 12 out of 34 varieties of peas, cultivated by Mendel, was not recorded in his final statement because amongst other drawbacks they exhibited "defective and irregular dominance" (I. p. 137).

By an analysis of this remarkable kind we are led to the statement that what is essential in Mendel's work is no ascertained fact at all, but Mr Bateson's peculiar interpretation of the hypothesis concerning the nature of germ-cells, which he calls "the great fact of gametic purity" (I. p. 117, II. p. 12).

3. *Atavism in hybrids.*—By rejecting dominance as "unessential," Mr Bateson is able to apply the theory of "pure" gamete formation to a number of cases in which the offspring of hybrids exhibit real or apparent reversion to the characters of the pure parental races, although nothing like dominance is seen in the hybrids themselves. But here he meets with a difficulty. In many of the newly-included cases the hybrids exhibit characters which suggest reversion to *remote* ancestors; for example, when von Guaita crossed pink-eyed albino mice with dark-eyed, black and white waltzing mice, he says that the hybrid young always resembled a wild mouse in size, colour, and wildness; here we have at least an apparent reversion to some characters of the common ancestors of both races. Again, Mr Bateson finds that there are several distinct races of Sweet Pea, which give rise to similar hybrids when crossed; and of these hybrids he says "it is characteristic of such "forms that they may reproduce *in appearance* some putative ancestor" (II. p. 144). It is not thought necessary to include facts like these, which surely depend upon the constitution of the germ-cells as much as any other phenomena of inheritance, in a theory of the gametes concerned. The apparent atavism is said to be peculiar to heterozygotes, and is so dismissed; its bearing on the phenomena of cross-breeding as a whole, and especially on "the great fact of gametic purity," being neglected.

We have here a second addition to Mendel's statements—the manifestation of a spurious atavism as a property of hybrids, and the doctrine that several different gametic combinations may produce identical individuals.

So far as I can discover, from an attempt to collate Mr Bateson's various statements, the only thing which can be predicated of the result of crossing pure races

is that the resulting hybrids, though their "character may be anything," will at least be uniform; this uniformity is indeed considered to differentiate Mendelian hybrids from those in which the ancestral characters are blended (II. p. 153).

4. *The similarity of reciprocal crosses.*—Mendel says that in all his experiments "it is perfectly immaterial whether the dominant character belong to the seed-"bearer or to the pollen-parent; the form of the hybrid remains identical in both "cases" (I. p. 50); and this, at least, seems "essential," because the law of segregation which he formulates to describe his results depends upon it. Mr Bateson however propounds a theory by which "the great fact of gametic purity" may apply to cases in which reciprocal crosses are unlike. He conceives a species in which the male gametes contain only one element A of a Mendelian pair, the female gametes containing only the complementary member a of the pair. When a male and female of such a species breed together, the fertilised zygote is of composition Aa; but the gametes produced by such a zygote will contain only A elements if the zygote body be a male, only a elements if it be a female. Each individual will therefore completely suppress half the heritage it receives from its parents during the course of its development. This novel and striking conception is not only completely foreign to Mendel but to all other naturalists, except Mr Bateson and his colleague Miss Saunders (II. p. 132).

The Horse and the Ass among animals, and certain species of *Digitalis* among plants, are adduced as examples of species between which the reciprocal crosses are unlike. If Mr Bateson's remarkable hypothesis be applied, it follows that in either the Horse or the Ass, and in some species of *Digitalis*, there are characters which cannot be transmitted from the female through a son to grand-daughters, others which cannot be inherited by grandsons from the maternal grandfather. With so rich a store of new and startling theories to propound, Mr Bateson naturally has no time to illustrate each of them in detail; but it would be interesting if he would spare a moment to tell us what these characters are in one of the cases he mentions.

5. *The behaviour of "compound characters" on crossing.*—The facts on which Mendel bases his theory of compound characters are these: A purple-flowered bean (*Phaseolus multiflorus*) was crossed with a white-flowered bean (*Ph. nanus*); from the account given we may assume that the hybrids produced were uniform in character, and we are told that whiteness of flower was completely recessive*. These hybrids, when self-fertilised, gave a whole series of flower colours; among 31 plants obtained, one had white flowers, the others had flowers of various shades from purple-red to pale violet. The experiment was not continued. The explanation offered is simple, and exhibits the phenomena observed as exactly parallel with those seen when Peas, of races which differ in two pairs of Mendelian characters, are crossed. Taking the well-known statements concerning the result

* I consider only Mendel's statements of flower-colour; the races differed, of course, in other characters, but the discussion of these is not immediately relevant.

of crossing a Pea of green (recessive) cotyledon colour and wrinkled (recessive) shape with one of yellow (dominant) colour and round (dominant) shape, and denoting the gametic elements by the initial letters of the qualities they represent, the gametes of one pea will on Mendel's view contain the elements $G + W$, those of the other $Y + R$. On cross fertilisation, each element of one gamete will unite with the complementary element of the other, to form a fertilised zygote element; the zygote will therefore be of constitution $(YG + RW)$. Now the plant resulting from this zygote will produce each of the elements Y, G, R, and W in equal numbers; and one member of each pair will be included in each gamete formed; a member of each pair will enter a given gamete independently of the member of the other pair; and there will result four kinds of gametes, each kind equally numerous, of composition $(Y + R)$, $(Y + W)$, $(G + R)$, and $(G + W)$; half the gametes of each kind will be of one sex, half of the other sex, and when self-fertilisation occurs, the gametes of opposite sexes will be mated at random. It is clear that the composition of the zygotes formed, and their relative frequency, will be represented by

$$\begin{array}{lll} (WW + YY), & 4(WR + YG), & (WW + GG), \\ 2(WW + YG), & 2(WR + GG), & (RR + YY), \\ 2(WR + YY), & 2(RR + YG), & (RR + GG). \end{array}$$

It will be noticed that only one individual dominant in both characters, and one recessive in both characters, occur in every 16 individuals.

Now Mendel assumes that the flower-colour of his purple bean is a combination of two or more entirely independent colour elements "which individually act like any other constant character of the plant," and he proceeds to treat each of these as if it were a separate unit character, like the shape or cotyledon colour of a pea. Supposing two such colour elements, A_1 and A_2, in the purple flower, he regarded the gamete of his *Ph. multiflorus* as containing these two elements $(A_1 + A_2)$, while the gamete of the white-flowered *Ph. nanus* contained two identical recessive white elements $(a + a)$. The constitution of the hybrid zygote he writes $(A_1a + A_2a)$ and as in the case of the peas referred to, he deduces nine possible forms among the descendants of such a zygote, occurring with the relative frequency

$$\begin{array}{lll} (A_1A_1 + A_2A_2), & 4(A_1a + A_2a), & (A_1A_1 + aa), \\ 2(A_1A_1 + A_2a), & 2(A_1a + aa), & (aa + A_2A_2), \\ 2(A_1a + A_2A_2), & 2(aa + A_2a), & (aa + aa). \end{array}$$

This treatment is quite similar to that of the simple unit characters of peas, in every respect but one. Every unit character in a pea is treated as if it were represented in the gamete by only a single element; but the simple unit character, whiteness, in *Ph. nanus*, is represented in the gamete by a number of similar unit elements equal to the whole number of dissimilar unit elements present in the compound character, purple, of the *multiflorus* flower. Admitting this, for the

moment, as a possibility, what happens when the same white-flowered *Ph. nanus* is crossed in one case with a coloured flower containing two unit colours, in another with a flower containing four or five?

Mr Bateson seems to have perceived this difficulty, and he has conceived what he calls a "compound allelomorph," the source of further complications. He conceives, if I understand him, that the colour-characters, A_1 and A_2 of a purple bean flower are not, as Mendel says, independent, but that they are combined, while in the pure-bred plant or its gametes, into a system which behaves like a single unit, so that he would, I think, agree to write the zygote, produced by crossing the purple-flowered and the white-flowered bean together, as $(A_1 + A_2)\, a$, where the portion enclosed in a bracket behaves like one unit character. Concerning the behaviour of a "compound allelomorph" when the hybrid forms its gametes, Mr Bateson has suggested a series of possibilities, each involving a process not included in Mendel's theory, and each incompatible with the view that a simple unit of colour character is comparable with "any other constant character of the plant." The principal suggestions so far put forward by Mr Bateson may be classified as follows:

A. *Suggestions in harmony with Mendel's view that elementary unit-characters are separated during gamete formation:*

(*a*) *The number of elements contained in the gametes produced by a hybrid need not be the same as the number contained in the pure parental gametes, and each gamete of hybrid origin may contain more than one element of the same kind.*

In this case Mr Bateson supposes that a hybrid zygote, of constitution $(A_1 + A_2 + A_3 + \ldots \text{etc.})\, a$ will, during gamete formation, give rise to a number of independent elements, A_1, A_2, etc., ... and a, and these will be distributed among the gametes; but he supposes that a gamete may be produced of constitution A_1A_1, A_2A_2, etc. (I. p. 80, II. p. 145). This is clearly not a phenomenon comparable with anything which can be supposed to occur when a zygote cross-bred from a green-wrinkled and a yellow-round pea produces gametes; for a gamete of constitution *YY* would have two elements determining cotyledon colour, and none whatever determining shape. The union of two such gametes would produce an unthinkable result, a pea with yellow colour and without shape; to aid our conception of such a pea we can only appeal to that "residue," the plant with all its unit characters removed, which Mr Bateson considers to be the foundation on which the idea of "Species" must ultimately rest! (I. p. 28, II. p. 148).

(*b*) *Each gamete produced by a hybrid contains one, and one only of the unit characters transmitted to it from its parents.* (*Proc. Cambridge Phil. Soc.* XII.)

In this case the heterozygote $(A_1 + A_2 + \ldots)\, a$ produces gametes of simple constitution A_1, A_2, ... or a, and here again we have a conception which cannot be applied to anything but colour without raising the difficulties pointed out in the case of the previous hypothesis. This second non-Mendelian hypothesis has so far been suggested in connection with two subsidiary suggestions:

(α) *The number of gametes of each kind is the same*; this is of course a Mendelian hypothesis.

(β) *The number of gametes, containing elements derived from the parent with simple character, is equal to the sum of all the other gametes, each of which has a single element of the compound parental character.* Here the view that gametes of all kinds are produced in equal numbers is given up, in order to fit a particular result.

It is important to notice that neither of the two hypotheses above described can be applied to any system of separable organs whose modifications are united to form a "compound allelomorph," without involving the production of an individual in which some of the characters are determined solely by that "residue" from which all unit characters are abstracted, pictured by Mr Bateson as the basis of our conception of Species. Yet he tells us that he has taken colour-characters as examples of the way in which other cases may be treated, because "the facts in those cases are clearer, but their nature is probably not different" (II. p. 146).

B. *The Mendelian theory, that all inherited characters are reduced to their elementary units and redistributed during gamete formation, is given up.*

Under this head we have two possibilities; for some gametes of the hybrid may contain the parental "compound allelomorph" *either* entire, *or* partly resolved into its constituents.

The doctrines put forward by Mr Bateson in connection with "compound allelomorphism" have been considered at some length, because of their great interest to anyone who wishes to appreciate his attitude. It must be remembered that no character can, on Mendel's view, be asserted *a priori* to be simple or compound. If a simple result, such as that obtained by Mendel when he crossed yellow and green peas, be obtained on crossing two animals or plants which differ in respect of any character, that character is simple, and there is no need to go further. Should the hybrids exhibit any unexpected character, a reference to the properties of "heterozygotes" will remove all difficulties; should the offspring of the hybrids be of more than two kinds, one or other of the foregoing hypotheses will generally be found to evade the difficulty; if not, "our conceptions of allelomorphic characters, simple and compound, are in process of formation*," and a new theory will quickly be provided.

We need not discuss the attempt to regard the sex of offspring as a phenomenon of gametic differentiation, a doctrine more difficult than even those we have described, excepting only that of the marvellous residue without unit characters, on which the future definition of species must be based. We may now proceed to examine the way in which Mr Bateson, after formulating all these hypotheses, treats Mr Darbishire's new facts.

* Bateson: "Note on the Resolution of Compound Characters by Cross-breeding." *Proc. Cambridge Phil. Soc.* XII. p. 53.

Mr Darbishire's Results and Mr Bateson's First Explanation.

The mice used by Mr Darbishire are normal pink-eyed albinos, of various ancestry, and a race of "Japanese" waltzing mice, having pink eyes and a piebald (fawn-coloured and white) coat. The normal albino mouse is said by Crampe, and by many mouse-breeders, to breed perfectly true, whatever its ancestry, and Mr Darbishire's albinos certainly so far do so. The waltzing mice also breed true in the sense that their offspring always waltz, and always have pink eyes with a fawn-and-white coat; but there are of course slight variations in the size and shape of the coloured patches. There is no proof that the results of reciprocal crosses between these two races are different. Therefore, since these two races each breed true, and give similar results in reciprocal crosses, they satisfy the conditions of "gametic purity" laid down by Mr Bateson, and there is no reason to assume that Mr Bateson's remarkable hypothesis of a difference in constitution between the male and female gametes applies to either.

The first hybrid generation, directly resulting from the cross, is so far constant in two respects; none of the individuals "waltz," and all have pigmented (dark) eyes. In coat-colour the hybrids are very variable; none have the fur entirely white, but the colour, and the extent of the coloured patches, vary widely. As to the amount of *white* fur; out of 203 mice available when Mr Darbishire's last Report was published, he tells me that one had *no* white fur; 69 had white on the belly only; 51 had some white on the back and sides, but less than in pure-bred waltzing mice; 30 had about the same amount of white as a waltzing mouse, and 3 had more. The colour of the coloured fur was *yellow* in 7 cases, a pale or dark "*wild-colour*," like that of the wild mouse, in 138 cases, and *black* in 9 cases.

The uniformly dark colour of the eyes is difficult to explain on any Mendelian hypothesis; for since pink eyes may coexist with a coloured coat, and dark eyes with a white coat, it is clear that in many cases at least eye-colour and coat-colour can be separately inherited, and should therefore on Mendel's view be represented by separate gametic elements. But we are told by Mr Bateson, and on better evidence by von Guaita, that albinism is a recessive character; and it seems natural to suggest that "albinism" is a "compound" character, composed of two or more elements, among which are whiteness of coat and pinkness of eye. On this view, the two purely recessive eye-colours of Mr Darbishire's mice should give pink eyes when crossed; and we see that they do not. No Mendelian hypothesis will account for the production of a new or atavistic eye-colour by the union of similar elements; and therefore, although eye-colour is certainly separable from whiteness of coat, because dark-eyed mice with white fur are well known; although it is similarly separable from a fawn-coloured-and-white coat, because among the offspring of Mr Darbishire's hybrids fawn-and-white individuals occur, some dark-eyed and some pink-eyed, yet a method must be devised by which this

darkness of the hybrid eye may be exhibited as a "property of heterozygotes," and so neglected, with the other inconvenient properties of first crosses, in applying the "great fact of gametic purity." Mr Bateson accordingly writes (*Nature*, No. 1742, March 19, 1903) "The first cross shows that when *in this case* an albino "(pink-eye) gamete, G, meets a colour-bearing (pink-eye) gamete, G', in fertilisation "we must expect the resulting heterozygote, GG', to be coloured in coat, with a "*dark* eye." Now if this means anything more than a mere re-statement of Mr Darbishire's result, it means that so far as coat-colour and eye-colour are concerned the elements in each gamete are to be treated as *single units*; they are either actually single, or they are "compound allelomorphs." The attempted explanation, even on this view, only succeeds in placing the phenomena in the same category with many others avowedly inexplicable, but it does avoid the difficulty of the origin of a new or atavistic character from the union of two similar eye-colour elements.

The coat-colour of the hybrids is still unexplained by Mr Bateson's statement; for since every hybrid by hypothesis results from the union of similar pairs of gametes, the hybrids themselves should be similar. Mr Bateson has hitherto assumed in all his discussions that whatever the characters of similar heterozygotes may be, at least they are similar! In this case, he passes over the difficulty in silence. To me (and I am glad to know that Mr Darbishire agrees with me) this variability of the hybrids is highly significant, when these results are compared with those obtained by others. Using a race of albinos, known to be absolutely pure because they had been inbred for 29 generations, and crossing these with pure-bred Japanese waltzing mice with dark eyes and black-and-white fur, von Guaita tells us that he obtained hybrids which uniformly resembled wild mice; making a similar cross, but using albinos of which no definite history is recorded, Haacke obtained hybrids sometimes like wild mice, and sometimes black. Mr Darbishire has deliberately used albinos which were sometimes pure-bred, sometimes known to have near ancestors of various colours, and he obtains a highly variable group of hybrids. Now the gametic purity of an extracted recessive form which breeds true cannot be questioned without abandoning the whole Mendelian position, or any modification of it, and therefore all these albino mice must be treated as equally pure, on Mr Bateson's view; but I submit that the three sets of facts already published by Mr Darbishire, by von Guaita, and by Haacke, show a correlation between the ancestry of the pure recessive albino and the character of the hybrids, sufficiently strong to disprove the "great fact of gametic purity" in this case, at least. The correlation between the colour of the coat in dominant hybrids, and in their hybrid grandchildren, which Mr Darbishire has shown to be established by transmission through a pure recessive albino, is still more conclusive evidence against the gametic purity of recessives, (*supra*, pp. 282–5).

So much for the result of the first cross. What happens when the hybrids of this generation are paired together? Mr Bateson represents the result as

a division of the second generation into three groups, of constitution and relative frequency indicated by the formula

$$GG + 2GG' + G'G'$$

where the homozygotes GG are pink-eyed albinos, the homozygotes $G'G'$ are pink-eyed "with some colour in the coat," and the heterozygotes GG' have "dark eyes "and some colour in the coat."

In this formula either coat-colour and eye-colour together are treated as a single unit character, or they are treated as a series of unit elements combined in a "compound allelomorph" which is transmitted to half the germ-cells of either sex completely unchanged, and the Mendelian principle that compound characters are reduced to their elements and redistributed in germ-cell formation is abandoned. The formula gives 25 per cent. pink-eyed albinos, 50 per cent. dark-eyed mice "with some colour in the coat," and 25 per cent. pink-eyed mice with some colour in the coat; the numbers given in Mr Darbishire's last Report, from which Mr Bateson deduced his formula, are

13 pink-eyed albinos,

36 dark-eyed with colour in the coat,

17 pink-eyed with colour in the coat,

and considering the small number of individuals, this record fits Mr Bateson's non-Mendelian formula very well. Any Mendelian hypothesis, which should attempt to account for the great variability in coat-colour by postulating a resolution of the "compound allelomorph" would lead to one of two results, either of which would be inconsistent with the experiments.

For if we suppose the elements which represent coat-colour and eye-colour to break up into only two components during the formation of gametes by the hybrid, then if both of these be supposed dominant over albinism, the number of pure albinos, or of pure dominants in the second generation is reduced to one in sixteen, a proportion which is not in accord with observation; if on the other hand one of the two colour elements be supposed recessive to albinism, we may get $\frac{3}{16}$ of the second generation showing albinism; such a proportion would fit the facts so far obtained, but two out of every three such albinos should be dominant hybrids, producing some coloured young, and no such albinos have been observed by Mr Darbishire or by any one else.

Mr Bateson's is therefore the only pseudo-Mendelian formula which will account for the observed distribution of eye-colour and albinism. But it is fatal to the "great fact of gametic purity," either in Mr Bateson's sense or in Mendel's. For this "great fact" involves much more than is implied by the statement that the $G'G'$ individuals are "pink-eyed, with some colour in the coat"; these individuals are said to be formed of gametes identical in constitution with those of their pure-bred waltzing grandparents, at least in respect of eye-colour and coat-

colour; the individuals produced from the union of such gametes should on Mendel's view be like individuals of the pure waltzing race, on Mr Bateson's view they should be "not like but identical with" their pure-bred waltzing grandparent, both in eye-colour and in coat-colour (II. p. 12). Now Mr Darbishire has pointed out (*Biometrika*, Vol. II, Part 2, pp. 167 and 168) that the mice, which Mr Bateson calls of constitution $G'G'$ may exhibit a blue-grey colour which breeders call "lilac," unknown in the pure-bred waltzing race (at least in the recent ancestry of the mice used) and equally unknown in hybrids of the first generation, which Mr Bateson calls GG'. At the time of writing, there are 18 mice of the group $G'G'$, all "pink-eyed, with some colour in the coat," and of these no less than six are either wholly or in part lilac.

The coat-colour of the 36 mice GG' is also variable, as is that of those mice (which Mr Bateson regards as having the same constitution) produced by crossing hybrids of the first generation with albinos. The variability of coat-colour, unaccompanied by a resolution of the allelomorph, is as great an obstacle to Mr Bateson's interpretation in this case as in the case of the first cross.

Here, as in so many other cases, a result in superficial agreement with those observed by Mendel can only be obtained by devising a series of categories so vaguely defined that they convey wholly inadequate information; and with a little skill such categories may be found to fit almost any series of results. Just as on a former occasion Mr Bateson has used the category "hairy" to imply identity of character between leaves in which the number of hairs per square centimetre may be anything from a dozen to over a thousand, so he here assumes that the conditions of equality, suggested when he asserts that 18 mice are of identical constitution $G'G'$, are satisfied when he has shown that they all have "pink eyes "and some colour in the coat." Such a category would include a pink-eyed mouse with green fur and a purple tail; and he makes it in fact include "lilac" and yellow.

Surely we want some better demonstration of the "identity" between pure dominants and their parents than this sort of category can give, before the "great "fact of gametic purity" can serve as a foundation for the huge superstructure of hypothesis built upon it!

When it is pointed out to Mr Bateson that he cannot legitimately class yellow, lilac, and black in a single colour category, he abandons his formula of March 19 and puts forward a new set of hypotheses (*Nature*, No. 1747, April 23, p. 585). He now explains the variability among Mr Darbishire's first crosses as due to gametic impurity in one or both of the races crossed. Now, apart from the difficulty of regarding a "pure recessive" albino as impure in the Mendelian sense, let us see whether the new statement fits the observed behaviour of the "pure" waltzing mice. The waltzing mice used by Mr Darbishire are chiefly descended from about 80 mice, 40 of each sex, bought by me some time ago, and paired at random under my direction. Now if we suppose these mice to have been impure in Mr Bateson's sense, that is, if we suppose them to have produced

gametes of more than one kind, this may have happened in either of two ways: there may have been two kinds of gametes, one kind produced by each sex, as supposed by Mr Bateson in the case of the Horse or the Ass, in which case the race would breed true, every individual being produced by a heterozygote which lost half its heritage during development. Such a form of gametic heterogeneity would be consistent with the observed fact that the mice bred true, but it would involve difference between the crosses Albino ♀ × waltzer ♂ and waltzer ♀ × Albino ♂ which has not been observed, and it would fail to account for the observed differences between individual hybrids produced by the same parents. The hypothesis that each mouse of either sex produces gametes of more than one kind involves *either* the hypothesis that these gametes do not obey Mendel's law at all, *or* that a constant percentage of "rogues," dominant or recessive in one or more elementary characters, is produced in each generation. No such rogues have been observed either in a very considerable number (many hundreds) of young examined before Mr Darbishire's experiments were begun or in pure waltzing families raised during the course of the experiments: so that this hypothesis also fails to fit the facts.

The second new assumption made by Mr Bateson, that coat-colour is a "compound" character, is probably true; but it completely fails to account for the observed variability among the offspring of the first cross, since no "resolution of compound characters" can occur during the formation of the first hybrid generation, and it involves a reduction of the number of pure recessive albinos, among the offspring of hybrids, to a *maximum* far below the observed proportion. Mr Bateson's new hypothesis therefore fails to fit the facts any better than his first.

I am as anxious as Mr Bateson can be to test the possible ways of bringing the behaviour of these mice into accord with Mendel's "principles" or indeed with any other theory of heredity. The two hypotheses already put forward fail, as we have seen. I earnestly appeal to Mr Bateson, now that the facts are fully before him, to produce some final formula, expressed in terms of categories so definite that they really describe the mice included, which seems to him capable of bringing the behaviour of these hybrid mice and their offspring into harmony with the "principles" he so strongly supports.

[A letter to *Nature*, May 14, containing a new hypothesis, has appeared while this article is going through the press. This letter and a paper before the Zoological Society of London, of which Mr Bateson has given notice, could not be discussed in the present number of *Biometrika* without unduly delaying its publication.]

MENDEL'S LAWS AND SOME RECORDS IN RABBIT BREEDING.

By FREDERICK ADAMS WOODS, M.D.

Owing to the current interest in Mendel's Laws of Heredity and the heated discussion going on in some quarters as to their validity, the following records from rabbit breeding may be of value, in showing what practical application the principles find when applied to a certain species of mammals not heretofore studied.

Within the last year many of the records formerly obtained by breeding mice have been gone over again in light of the Mendelian principles, and in some instances there is a clear uniformity with what might be expected, notably the point that albinism is pure recessive and always when mated with itself gives rise to albinos and nothing else. (Crampe (5) and von Guaita (8).) The waltzing character is also recessive according to Bateson, who in his recent book, *Mendel's Principles of Heredity* (p. 174), discusses this point. It is, however, not clear that all the results of different observers can be harmonized with the Mendelian principles. (Conf. Weldon (10) p. 244.)

In view of this condition of the subject further studies of the old material, as well as new records among other groups of mammals, must be made before we shall know what practical application the experiments of the botanists, Mendel, de Vries, Correns, Spillman, and others will have when applied in the breeding of animals, or what will be the importance of these remarkable laws to the student of heredity in its widest scope.

Rats and mice are excellent material for use in this connection as they breed true to certain definite types, and do not easily blend. The same is true of rabbits. The progeny of crosses illustrate "alternative" inheritance, each off-

spring resembling in colour some one parent or other ancestor, rather than a mixture of many. As this is equally true of common pet rabbits, these animals should be good material to furnish evidence for the Mendelian principles.

The following experiments on the colour inheritance of rabbits were originally undertaken in order to get exact material for the study of Galton's Law of Ancestral Heredity (9); and were begun in the spring of 1899. Up to the present time I have bred some 350 young, most of whom have ancestry now kept to the third or fourth generation, yet there has always been such a marked deviation from the law as announced by Galton that I have wished to withhold the results until a larger number of figures might be at hand. Thinking, however, that if Mendel's principles are to be of practical application to the breeder, they should show their force in a group of at least 300 individuals, I determined to see what help might be derived by using this old and forgotten work now so fortunately rediscovered.

My original purpose was to obtain by means of artificial selection a race of pure blacks and then cross these with albinos. Although I have selected the blacks with this end in view for several generations a pure black race has not yet been formed. This part of the work then is very similar to the efforts of a breeder of fancy stock, trying to improve his strain. Most of the other experiments are the crossing of nearly pure black with albinos, or the mating of albinos which have black in the ancestry. I have always felt that it was very strange that two albino parents which are themselves the descendants of an ancestry almost entirely black on all sides, should never be able to throw a trace of black in any of their progeny. Such a fact being absolute in every instance cannot be passed over by calling it "a prepotency," since if there were a prepotency of white over black, the black ought, nevertheless, once in a while to show itself, which under these circumstances it never does, according to both the reports of breeders and the records of investigators.

We may now turn to the analysis of the figures, taking the three main groups according to colour of parents: 1st, black × black; 2nd, black × white; 3rd, white × white.

The colours met with are indicated as follows: B = black; W = albino; G = grey; Y = yellow. A few spotted ones which could not be placed in any one of these categories were occasionally met with; these will be described in detail.

The number of each experiment (or litter) is given in Roman numerals. The numbers in brackets, e.g. (1) (2) etc. are used to distinguish the individual rabbits.

The 150 offspring when both parents were black or nearly so, were 105 of similar colour; 28 albino; 9 grey; and 8 yellow. Intermediate or spotted forms did not occur from these pairings.

We analyse the results of mating Black with Black in Table I.

TABLE I.

Black × *Black.*

	Parents		Offspring			
	♂	♀	*B*	*W*	*G*	*Y*
i	(1)	(2)	4	—	1	2
ii	(7)	(3)	5	1	—	—
iii	(1)	(14)	3	—	—	—
iv	(1)	(2)	5	—	—	1
vii	(1)	(14)	3	1	—	—
viii	(7)	(28)	2	1	—	—
xi	(7)	(6)	2	—	—	—
xiii	(7)	(28)	2	1	1	—
xiv	(7)	(5)	3	—	—	—
xv	(7)	(6)	1	—	—	—
xviii	(32)	(2)	4	1	—	—
xix	(21)	(34)	2	2	1	—
xx	(21)	(37)	5	1	—	—
xxi	(33)	(6)	4	1	—	—
xxiv	(32)	(20)	4	—	—	—
xxv	(32)	(2)	2	—	—	2
xxvi	(21)	(37)	3	1	—	—
xxvii	(21)	(34)	2	—	—	—
xxviii	(32)	(20)	3	3	—	—
xxix	(54)	(51)	4	—	—	—
xxx	(50)	(5)	4	—	2	—
xxxi	(21)	(37)	2	3	2	—
xxxiii	(21)	(37)	4	2	1	—
xxxvi	(115)	(51)	4	—	—	—
xxxvii	(32)	(37)	3	1	1	1
xliii	(32)	(37)	3	1	—	1
xliv	(32)	(116)	1	1	—	—
xlviii	(121)	(132)	2	1	—	1
xlix	(32)	(37)	4	—	—	—
li	(32)	(116)	3	1	—	—
lvi	(32)	(116)	3	3	—	—
lxiv	(131)	(116)	6	1	—	—
lxviii	(131)	(116)	3	1	—	—
			105	28	9	8
			Total 150			

It can be seen after a careful survey of the parents that there were four rabbits used who gave no white when mated with any other. These were (5), (50), (51), and (54). The others, since they at some time were parents of one or more albinos, must have had albinism recessive, if the Mendelian principle be correct.

There were 17 offspring born from (5), (50), (51) and (54). (5) × (7) = 3; (5) × (50) = 6; (54) × (51) = 4; (115) × (51) = 4. Subtracting these 17 we

then have 133 young, the descendants of the mating of black parents, who in the Mendelian sense are known to have albinism recessive.

Of these 133 young 28 only were albinos. 25°/₀ should have been if Mendel's law is correct, for the product of $DR \times DR$ should be $D + 2DR + R$. Or in other words, three-fourths should appear with the dominant colour, in two-thirds of which the white is recessive but not manifest.

$$\frac{28}{133} = 21{\cdot}05\,\%_0 \text{ instead of } 25\,\%_0.$$

Results of Black crossed with White or *vice versa* are shown in Table II.

TABLE II.

Black × *White.*

	Parents		Offspring				
	♂	♀	*B*	*W*	*G*	*Y*	
xii	(7) *B*	(40) *W*	1	2	—	—	—
xxiii	(21) *B*	(38) *W*	2	2	—	—	—
xxxv	(112) *W*	(85) *B*	4	2	—	—	1*
xxxviii	(112) *W*	(85) *B*	2	3	—	—	—
xli	(112) *W*	(85) *B*	1	5	—	—	—
xlii	(112) *W*	(51) *B*	3	—	—	—	—
xlv	(112) *W*	(85) *B*	2	1	3	—	3†
liv	(112) *W*	(85) *B*	5	1	—	—	1‡
lvii	(124) *B*	(139) *W*	1	—	—	—	—
lviii	(124) *B*	(139) *W*	3	—	—	—	—
lxix	(112) *W*	(85) *B*	3	3	—	—	—
lxvi	(112) *W*	(85) *B*	1	1	—	—	—
lxxi	(112) *W*	(85) *B*	1	2	—	—	2‡
lxxiv	(112) *W*	(85) *B*	5	3	—	—	—
Totals	—	—	34	25	3	—	7

* 3/4 *W*, 1/4 *B*. † 4/5 *W*, 1/5 *B*. ‡ Spotted.

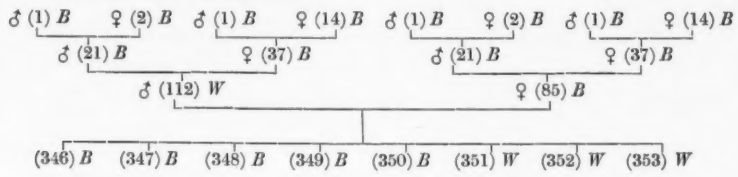
Rabbit (51), suspected of being a pure dominant in the $B \times B$ matings, occurs here once, therefore her litter, as well as the four from (124) may be taken out, since we cannot be sure that these, as parents, contained any white recessive.

If these seven young are taken out of the consideration it will be seen that 27 *B*; 25 *W*; 3 *G*, and 7 spotted were born from $DR \times R$.

The product of $DR \times R$ according to Mendel should give equal numbers of *D*s and *R*s (conf. Bateson (2) p. 158). The figures are 25 albinos in 62 or 40·3°/₀ instead of 50°/₀. Here as before the error is on the side of too little white in the offspring.

In most of these the back ancestry was black. A characteristic pedigree lxxiv is shown below, where it will be seen that one white in every two, which

is demanded by Mendel's Law, would not be expected from Galton's. A less amount of white would be called for by the latter law on account of the influence of grandparents and great-grandparents. Hence the error from Mendel's Law may be due to ancestral influence.



Results of White crossed with White are shown in Table III.

TABLE III.

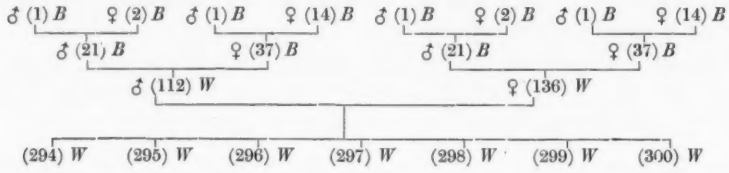
White × *White.*

	♂ and ♀ Parents both albinos	*B*	*W*	*G*	*Y*
ix	(38) × (39)	—	6	—	—
x	(38) × (39)	—	4	—	—
xvi	(46) × (40)	—	4	—	—
xxii	(46) × (40)	—	3	—	—
xxxii	(46) × (40)	—	7	—	—
xxxiv	(112) × (38a)	—	6	—	—
xxxix	(112) × (120)	—	5	—	—
xl	(112) × (120)	—	5	—	—
lii	(112) × (136)	—	4	—	—
lv	(112) × (36)	—	5	—	—
lx	(112) × (136)	—	6	—	—
lxii	(112) × (120)	—	6	—	—
lxiii	(112) × (136)	—	7	—	—
lxv	(112) × (136)	—	1	—	—
lxvii	(112) × (120)	—	4	—	—
lxix	(112) × (136)	—	3	—	—
lxx	(112) × (136)	—	5	—	—
lxxiii	(112) × (136)	—	5	—	—
Total	—	—	86	—	—

Here we have 86 offspring, all albinos. This is of course in keeping with Mendel's principles, since $R \times R$ can give only R. It is not in harmony with Galton's Law, and especially so in this instance, since all the latter two-thirds of the experiments were made with the three rabbits (112), (120), and (136), who had two black parents, and four black grandparents as well. These animals have been intentionally used to see if some black reversions might not be obtained from such a curious mating.

The pedigree of experiment lxiii is given below, and is characteristic of the rest, and can hardly be explained in any other way than recourse to the

Mendelian principles. The buck and doe albino, brother and sister, were closely inbred from black stock.



In addition to the foregoing a few crosses were made between the white buck (112) and a brownish yellow (108), herself the descendant of black ancestry.

Table IV brings out the curious fact that among 19 of her young, her own colour does not appear at all.

TABLE IV.

	Parents	Offspring			
	♂ *B* ♀ *Y*	*B*	*W*	*G*	*Y*
liii	(112) × (108)	1	3	1	—
lxi	(112) × (108)	4	1	1	—
lxxii	(112) × (108)	3	5	—	—
Totals	—	8	9	2	—

Such a result continually obtained would not be in keeping with Galton's Law, since at least 25 °/₀ of the offspring ought to be yellow as a result of the influence of one of two parents. It can perhaps be explained by Mendel's principles when a further knowledge of coloration enables us to say how yellow is broken up when combined with pure gametes like those produced from albinos. This may be similar to the "mosaic inheritance" described by Castle (3) and (4).

I have made as yet no accurate correlations to test the Galton-Pearson Law of Ancestral Heredity, as I wish to have later generations giving a more complete back pedigree and larger figures, before such is attempted. Rough draughts, however, show that there is a wide discrepancy of from 15 °/₀ to 25 °/₀ from the calculated.

In the case of *W* × *W* this is even worse, since the amount of black in the grandparents and great-grandparents calls for 30 °/₀ to 45 °/₀ black in offspring, whereas we find none at all. The experiments, therefore, confirm the idea that the Law of Ancestral Heredity will not hold so well in cases of alternative inheritance as it does when applied to characteristics which freely blend.

The results set forth in Davenport's review of von Guaita's experiments (8) in breeding mice are also confirmed.

It is however to be noticed that the deviations from Mendel's Law in Tables I and II, namely too little white, are on the side of suggesting an ancestral influence which Mendel's Law does not recognize. This neglect of ancestry Weldon considers to be the fallacy of the Mendelian principles, and writes as follows (10), p. 252.

"The fundamental mistake which vitiates all work based upon Mendel's method is the neglect of ancestry and the attempt to regard the whole effect upon offspring, produced by a particular parent, as due to the existence in the parent of particular structural characters; while the contradictory results obtained by those who have observed the offspring of parents apparently identical in character show clearly enough that not only the parents themselves, but their race, that is their ancestry, must be taken into account before the results of pairing them can be predicted."

It certainly would seem that as regards the breeding of mammals we cannot with our present knowledge give up the idea that ancestry has some influence.

This influence of ancestry is contended for by Darbishire (7)* in a short article in *Biometrika* in which he clearly shows the influence of ancestry in a number of crosses between the Japanese waltzing and albino mice. It seems in every one of a few instances given to make a considerable difference in the results whether his albinos are from pure-bred stock or not. Perhaps further experiments may show what characteristics are pure *unit-characters*†, as albinism appears to be, and then all results will agree closely with the expected.

Or, on the other hand, further experiments may overthrow the reliance to be placed on the few figures already collected. At any rate, the future only can decide. The figures given in this article show more than anything else, that any law yet formulated, when applied to an instance similar to practical stock improvement, gives results not remarkably in keeping with the observed. In this case the truth seems to lie between the expected as announced by Mendel and that formulated by Galton.

Before closing it might be interesting to compare the figures, 21 %, obtained from rabbits by $DR \times DR$ with those of other observers for mice. Crampe (5), p. 542, crossed grey wild mice with albinos and obtained 15 young, all resembling the wild form. The next generation gave 79 young, 22 of whom were albino. $\frac{22}{79} = 27{\cdot}8\ \%$. Von Guaita (8), (p. 122 Davenport's review), shows under similar conditions 14 albinos out of 44, or 31·8 %. Cuénot (6), out of 270 young, 72 albino, or 26·6 %; and again 162 grey to 57 albino, or 26 %. Thus all the figures range between 21 and 31·8 %, and seem pretty close considering the comparatively small numbers used.

As was stated above, my result for $DR \times R$ is not so close as that for $DR \times DR$; and instead of 50 % R we find 40·3 %.

* Since writing a second article by Darbishire has appeared.

† Bateson (1), p. 27, discusses "unit-characters."

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UEBER ASYMMETRIE BEI "GELASIMUS PUGILATOR" LATR.

Von GEORG DUNCKER, Ph.D.

Die vorliegende Arbeit soll einen Beitrag zur Kenntniss der Abhängigkeit der individuellen Symmetrieverhältnisse verschiedener Paare bilateral-homologer Merkmale von einander liefern. Bei symmetrischen sowohl wie bei asymmetrischen derartigen Merkmalpaaren bilateral gebauter Organismen sind die Unterschiede ihrer Einzelmerkmale mit Nothwendigkeit variabel, sofern diese Einzelmerkmale selbst variabel sind und zu einander in unvollständiger Korrelation stehen. Man erhält also bei der statistischen Untersuchung numerisch ausdrückbarer, bilateral-homologer Merkmale ungleiche individuelle Differenzen derselben, deren Zusammenstellung eine den Variationsreihen ähnliche Reihe, die Differenzreihe des Merkmalpaares, ergiebt. Die Differenzen verschiedener Grösse entsprechen den verschiedenen Graden individueller Symmetrie resp. Asymmetrie des Merkmalpaares; seine Kollektiv-Symmetrie, resp. Asymmetrie bei der untersuchten Formengemeinschaft wird nach dem durchschnittlichen Verhalten der Differenzreihe beurtheilt. Dadurch dass man bisher ausschliesslich das letztere, nicht aber die thatsächlich existirenden Einzeldifferenzen zu berücksichtigen pflegte, entstand z. B. die irrige Auffassung von der spiegelbildlichen Aehnlichkeit bilateral-homologer Organe bei symmetrischen Thierarten.

Wie ich bereits an einzelnen Beispielen nachgewiesen habe [1.] und demnächst an einem umfangreicheren Vergleichsmaterial darzuthun beabsichtige, sind in der Regel die individuellen Symmetrieverhältnisse verschiedener Merkmalpaare von einander mehr oder weniger unabhängig; es besteht keine nennenswerthe Korrelation zwischen ihren Differenzreihen. Das im Folgenden zu besprechende Material bietet gewisse Abweichungen von dieser Regel und ist überdies dadurch besonders instruktiv, dass bei ihm Dimorphismus der Kollektiv-Asymmetrie vorliegt; es kommen entweder rechts- oder linksseitig asymmetrische, dagegen keine symmetrischen Individuen vor.

1901 veröffentlichte Robert M. Yerkes eine Abhandlung [2.]: "A study of Variation in the Fiddler-Crab (*Gelasimus pugilator* Latr.)." Die Männchen der

Gelasimus-Arten sind durch den Besitz zweier hochgradig differenzierter Scheeren ausgezeichnet. Eine von ihnen ist verhältnissmässig sehr gross, auffällig gefärbt, mit Zähnen bewehrt und dient nach Yerkes (p. 440) sowohl zur Vertheidigung als auch zum Graben, in vielen Fällen wohl auch zum Anlocken der Weibchen. Die andere Scheere ist zwerghaft, unscheinbar gefärbt, unbezahnt und dient zum Zuführen der Nahrung in den Mund. Wir wollen die beiden im Folgenden als Kampf- und als Fressscheere unterscheiden. Die Weibchen weisen stets nur zwei kleine, übereinstimmende Fressscheeren auf.

Die Stellung der Kampf- zu der Fressscheere bei den Männchen wechselt derart, dass jene bald der rechten, bald der linken Körperseite angehört; wir theilen dann nach der Stellung der Kampfscheere die Gesammtheit der Männchen in zwei Gruppen, die Rechts- (*R*) und die Linkshänder (*L*) ein. Beide sind ungefähr gleich häufig, denn Yerkes (p. 424, Tab. III, IV) fand in West Falmouth Harbor:

	bei *Gelasimus pugilator*		*Gelasimus pugnax*	
am	*R*	*L*	*R*	*L*
18—22. VIII. 99	501 = 51·9%	465 = 48·1%	—	—
16. VII. 00	431 = 50·0%	431 = 50·0%	552 = 48·8%	578 = 51·1%

Aus Yerkes' Untersuchungen ergeben sich neben den sehr ausgeprägten Ungleichheiten der bilateral-homologen Scheerendimensionen auch noch schwächere der Längen der beiden Lateralränder (*M*) des Cephalothorax-Panzers und der beiderseitigen Meropoditen (*G*) des zweiten Beinpaares (= 1. Gangbeinpaares). Die an dem Scheerenpaare gemessenen Dimensionen sind Längen der Meropoditen (*Ch*), der Carpopoditen (*C*) und der Propoditen (*P*) von ihrer Basis bis zum Gelenk des Daktylopoditen. Endlich waren an jedem der je 400 untersuchten rechts- und linkshändigen Thiere die Medianlänge des Panzers (*T*) und seine Orbitofrontalbreite (*F*) zwischen den vorderen Seitenzähnen auf 0·1 mm. gemessen worden; cf. Yerkes' Figg. 1 u. 2 (pp. 419—420), sowie seine Beschreibung des Messungsverfahrens (p. 420).

Es lag nun der Gedanke nahe, dass die Ungleichheiten der einzelnen Dimensionen Folgen der Scheerendifferenzirung seien, da ja bereits die Gewichtsverschiedenheit der Scheeren sehr wohl zu Ungleichheiten der einzelnen Merkmale auf den beiden Körperseiten Anlass geben könnte. War diese Annahme richtig, so stand zu erwarten, dass auch ihre individuellen Unterschiede, im Gegensatz zu anderweitigen Befunden, korrelativ von einander abhängig seien. Auf diesen Punkt also richteten sich die Untersuchungen, deren Resultate im Folgenden mitgetheilt werden sollen.

Herr Yerkes hatte die grosse Liebenswürdigkeit, mir auf meine Bitte seine handschriftlichen Messungstafeln, welche 400 *R*- und 400 *L*-Thiere enthalten, leihweise zu überlassen. Die auf 0·1 mm. ausgeführten Einzelmessungen derselben fasste ich zu solchen von 0·5 mm. Varianteneinheit derart zusammen, dass z. B. 7·3—7·7 mm. = 7·5 mm. = 15 $\frac{\text{mm.}}{2}$, 7·8—8·2 mm. = 8·0 mm. = 16 $\frac{\text{mm.}}{2}$

gesetzt wurden, und berechnete aus den so entstandenen reducierten Variationsreihen deren Bestimmungswerte sowie die Korrelationskoeffizienten der paarigen Merkmale. Aus den für die Berechnung der letzteren nothwendigen Kombinationsschemata ergaben sich durch einfache Auszählung die absoluten Differenzreihen der bilateral-homologen Merkmalpaare (s. Anhangstab.), deren Bestimmungswerthe zu denen der beiden Variationsreihen der Einzelmerkmale I und II in folgenden einfachen Beziehungen stehen:

$$A_D = A_I - A_{II}, \quad \sigma_D = \sqrt{\sigma_I^2 + \sigma_{II}^2 - 2\rho\,\sigma_I\,\sigma_{II}},$$

$$\beta_{3D} = \frac{\Sigma(x_I^3) - \Sigma(x_{II}^3) - 3\,\Sigma(x_I^2 x_{II} - x_I x_{II}^2)}{n(\sigma_I^2 + \sigma_{II}^2 - 2\rho\,\sigma_I\,\sigma_{II})^{\frac{3}{2}}},$$

$$\beta_{4D} = \frac{\Sigma(x_I^4) + \Sigma(x_{II}^4) + 6\,\Sigma(x_I^2 x_{II}^2) - 4\,\Sigma(x_I^3 x_{II} + x_I x_{II}^3)}{n(\sigma_I^2 + \sigma_{II}^2 - 2\rho\,\sigma_I\sigma_{II})^2}.$$

Die benannten Bestimmungswerthe (A und σ) der Variations- und der Differenzreihen sind, wie die Varianten derselben, im Folgenden stets in der Varianteneinheit $u = 0{\cdot}5$ mm. ausgedrückt.

Die Berechnung der Korrelationskoeffizienten erfolgte nach Bravais' Formel in Pearson's Vereinfachung des Rechenprozesses

$$\rho = \frac{\Sigma(x_I x_{II})}{n\,\sigma_I\sigma_{II}} = \frac{\frac{1}{n}\Sigma([V - V_0]_I \cdot [V - V_0]_{II}) - V_I\,V_{II}}{\sigma_I\sigma_{II}},$$

wo $$x_I = (V - A)_I \text{ und } V_I = \frac{1}{n}\Sigma(V - V_0)_I.$$

Die Beziehung zwischen ρ, σ_D, σ_I und σ_{II} diente zur Kontrole der vorherigen Rechnung nach der Formel

$$\rho' = \frac{\sigma_I^2 + \sigma_{II}^2 - \sigma_D^2}{2\sigma_I\sigma_{II}}.$$

Häufig stimmten die für ρ und ρ' gefundenen Werthe noch auf fünf Dezimalen überein und niemals erreichte die Differenz derselben eine Einheit der vierten Dezimalstelle. Ihr wahrscheinlicher Fehler nach der Formel

$$p\,.\,\Sigma_\rho = \frac{(1 - \rho^2)\,.\,0{\cdot}67449}{\sqrt{n}}$$

ermittelt, wurde den einzelnen Korrelationskoeffizienten hinzugefügt. Sämmtliche für die vorliegende Arbeit in Betracht kommende Kombinationsschemata (30) sind bei dem Herausgeber dieser Zeitschrift hinterlegt.

Da zwischen der Totallänge und der Orbitofrontalbreite sehr hohe Korrelation besteht, nämlich für

	Rechtshändige	Linkshändige
ρ	$0{\cdot}91711 \pm 0{\cdot}00536$	$0{\cdot}90085 \pm 0{\cdot}00636$

so benutzte ich diese beiden Dimensionen gleichzeitig, um das Material in drei Grössengruppen zu zerlegen, für deren mittlere T 23 bis 26 $\frac{\text{mm.}}{2}$, F 30 bis 32 $\frac{\text{mm.}}{2}$ inclusive beträgt. Ein Uebergreifen der kleinsten Gruppe mit einer dieser Dimensionen in das Gebiet der grössten oder umgekehrt fand in Folge der bedeutenden Korrelation nicht statt.

Soweit bisher statistische Untersuchungen bilateral-homologer Merkmalpaare vorliegen, ergeben dieselben ausnahmslos unvollständige Korrelation variabler Merkmale. Hieraus und aus den Beziehungen der Bestimmungswerthe der Differenzreihe zu denen der Variationsreihen der Einzelmerkmale folgt, dass der Grad der individuellen Asymmetrie variabel ist, dass also neben symmetrischen stets auch asymmetrische Individuen hinsichtlich des Merkmalpaares auftreten müssen. Die Kollektiv-Symmetrie eines Merkmalpaares kann daher nicht wohl auf dem "spiegelbildlich gleichen Verhalten der beiden Körperseiten zu einander" beruhen, sondern sie ist, wie in [1.] gezeigt, definiert durch eine symmetrische Differenzreihe mit dem Mittel Null. Ist nun eine Differenzreihe um Null als Mittel symmetrisch, so ist auch ihr Centralwerth gleich Null, folglich sowohl die Anzahl als auch die Summe der positiven gleich der der negativen Differenzen, wenn letztere ihrem absoluten Zahlenwerth nach gerechnet werden. Für dies Verhalten aber haben wir als einfachen Ausdruck den *Asymmetrieindex* der Differenzreihe

$$\alpha = \frac{\Sigma(f').\Sigma(D') - \Sigma(f'').\Sigma(D'')}{n[\Sigma(D') + \Sigma(D'')]} = 0,$$

wo mit f' und D' Frequenz- resp. Differenzwerthe des positiven, mit f'' und D'' die entsprechenden Werthe des negativen Abschnittes der Differenzreihe bezeichnet sind. Existieren dagegen nur positiv oder nur negativ asymmetrische, aber keine symmetrischen Individuen, so wird $\alpha = \pm 1$, d. h., es liegt vollkommene positive oder negative Asymmetrie des Merkmalpaares bei der untersuchten Individuengemeinschaft vor. Das Vorzeichen des Asymmetrieindex entspricht den bei bilateralen Organismen denkbaren einander entgegengesetzten Möglichkeiten der Kollektiv-Asymmetrie, z. B. rechts- oder linksseitig, oder, in unserem Falle, auf der Kampf- oder der Fressscheerenseite überwiegende Entwicklung der homologen Merkmale. Der Asymmetrieindex* stellt somit den kürzesten Ausdruck der Kollektiv-Asymmetrie eines Merkmalpaares bei einer Individuengemeinschaft dar.

* Rechnungsbeispiel: Absolute Differenzen der Lateralränder bei den Rechtshändern. (Cf. Anhangstab.)

D=Md—Ms:	−1	0	1	2	3
f:	1	63	310	23	3

$\Sigma(D') = 310 \times 1 + 23 \times 2 + 3 \times 3 = 365$, $\Sigma(f') = 336$,

$\Sigma(D'') = 1$, $\Sigma(f'') = 1$, $n = 400$,

$$\alpha = \frac{336 \times 365 - 1 \times 1}{400 \times 366} = \frac{122639}{146400} = 0{\cdot}83770.$$

Da die Variationsreihen der untersuchten Merkmale gegenüber den in Yerkes' Arbeit angeführten ([2.], p. 42 Tab. I u. Figg. 1—12) durch die Reduktion der Messungen auf 0·5 mm. etwas verändert erscheinen, gebe ich zunächst eine Zusammenstellung ihrer Bestimmungswerthe, nämlich ihr arithmetisches Mittel (A), ihren Variabilitätsindex (σ), beides in halben Millimetern als der Variantenein heit ausgedrückte Zahlen, ihren dritten* (β_3) und ihren vierten Momentquotienten (β_4), welche unbenannte Zahlen sind. Ferner habe ich die Quartilwerthe Q_1 und Q_3, deren arithmetisches Mittel q, und den Medianwerth M für Totallänge und Orbitofrontalbreite aufgeführt.

TABELLE I.

R, L, =rechtshändige resp. linkshändige Thiere. s (sinister), d (dexter)=linke oder rechte Körperhälfte.

				A	σ	β_3	β_4	δ
Dimensionen des Panzers	Medianlänge (T)		R	24·48750	1·76489	0·57873	3·46339	—
			L	24·45000	1·82414	0·47809	3·36645	—
	Orbitofrontalbreite (F) ...		R	31·44250	2·24537	0·73608	3·42996	—
			L	31·26750	2·44457	0·58306	3·32595	—
	Lateralränder (M)...	R	s	16·76750	1·46234	0·54573	3·21308	25·11%
			d	17·67750	1·54386	0·60112	3·45931	
		L	s	17·37750	1·57321	0·49973	3·38461	25·18%
			d	16·54250	1·47587	0·64010	3·37943	
Meropoditenlänge des 1. Gangbeinpaares (G) ...		R	s	14·22750	1·25329	0·63178	3·29739	29·17%
			d	15·14500	1·39247	0·57075	3·39429	
		L	s	15·11250	1·49159	0·52587	3·25918	30·84%
			d	13·95750	1·32125	0·40979	3·11063	
Dimensionen des Scheerenpaares	Meropoditenlänge (Ch)	R	s	11·08750	1·02462	0·45204	2·96605	97·88%
			d	17·50500	1·59540	0·39896	3·09451	
		L	s	17·27000	1·68288	0·34230	3·25285	98·03%
			d	10·59500	1·02761	0·42801	3·23408	
	Carpoditenlänge (C)	R	s	6·09750	0·63482	0·32710	3·48979	100·00%
			d	14·23750	1·50036	0·60851	4·09883	
		L	s	13·72000	1·38802	0·35723	3·29010	100·00%
			d	5·94000	0·66813	0·32044	3·07763	
	Propoditenlänge (P)	R	s	5·43750	0·54872	0·29404	2·26207	100·00%
			d	18·45500	1·89023	−0·06681	3·72480	
		L	s	18·05750	1·82049	−0·04050	3·22911	100·00%
			d	5·50750	0·59156	−0·01074	2·53760	

* $\beta_3 = \frac{\Sigma(x^3)}{n\sigma^3} = \pm\sqrt{\beta_1}$ (Pearson).

ANHANG ZUR TABELLE I.

Erste und dritte Quartilwerthe (Q_1 u. Q_3), sowie deren Mittelwerth (q), und Medianwerthe (M) der Panzerlänge und Orbitofrontalbreite.

		Q_1	M	Q_3	q
Panzerlänge (T) ...	R	23·26623	24·24545	25·57547	1·15462
	L	23·21429	24·24074	25·59434	1·19003
Orbitofrontalbreite (F)	R	29·92169	31·09770	32·45588	1·26710
	L	29·72989	30·94000	32·46667	1·36839

Die Durchschnittswerthe fast sämmtlicher untersuchten Merkmale sind bei den rechtshändigen Thieren grösser, als bei den linkshändigen; die einzige Ausnahme bildet der Propodit der Fressscheere. Die Durchschnittswerthe aller paarigen Merkmale sind auf der Seite der Kampfscheere grösser, als auf der der Fressscheere.

Die Variabilität der Merkmale ist meistens bei den linkshändigen Thieren bedeutender; Ausnahmen bilden der Carpopodit der Kampfscheere und vielleicht auch ihr Propodit. Wie die Durchschnittswerthe der paarigen Merkmale, so sind auch ihre Variabilitätsindizes stets grösser auf der Seite der Kampfscheere.

Die dritten Momentquotienten sind meistens positiv; negativ nur für die Propoditenlänge der Kampfscheere bei Rechts- und Linkshändern, sowie vielleicht bei letzteren für die der Fressscheere, wo er jedoch kaum von Null verschieden ist. Ihrem absoluten Werth nach bleiben sie sämmtlich unter 0·65, sind also nur klein. Bestimmte Grössenbeziehungen hinsichtlich ihrer bei Rechts- und Linkshändern, sowie auf den homodynamen Körperseiten bestehen nicht, obwohl sie im allgemeinen bei rechtshändigen etwas höher sind als bei linkshändigen Thieren.

Die vierten Momentquotienten sind meistens bei den Rechtshändern grösser, als bei den Linkshändern; ausgenommen sind hiervon diejenigen des Lateralrandes auf der Seite der Fressscheere und der beiderseitigen Scheerenmeropoditen. Die der paarigen Merkmale sind stets auf der Seite der Kampfscheere grösser, stimmen also hierin mit dem Verhalten von A und σ überein.

Die Variationsgebiete der Lateralränder und die der Meropoditenlängen des zweiten Beinpaares fallen weitgehend zusammen, wie aus der verhältnissmässig kleinen prozentualen Differenzfläche ihrer Variationspolygone hervorgeht. Die der chelaren Meropoditenlängen greifen noch ein wenig ineinander über, während jene der übrigen bilateral-homologen Merkmale vollständig getrennt sind. Demnach erscheint bei dem vorliegenden Material das gemeinsame Variationsgebiet zweier bilateral-homologer Merkmale um so grösser, je näher dieselben einander am Körper der Thiere liegen.

Parallel zu dem letzterwähnten Verhalten geht das der Korrelationsintensität zwischen den paarigen Merkmalen. Ihre nachstehend aufgeführten stets positiven

Korrelationskoeffizienten schwanken zwischen 0·95 (Lateralränder) und 0·47 (chelare Propoditen), also innerhalb eines weiten Spielraumes, bald bei Rechts-, bald bei Linkshändern etwas überwiegend. Die Beziehung der Korrelationsintensität zur räumlichen Anordnung der bilateral-homologen Merkmale erscheint mir besonders beachtenswerth.

TABELLE II.

Korrelationskoeffizienten zwischen rechter und linker Körperseite.

R = rechtshändige, L = linkshändige Thiere.

	R	L
Laterale Panzerränder	0·94678 ± 0·00349	0·94976 ± 0·00330
Meropoditenlänge des 1. Gangbeinpaares	0·91796 ± 0·00531	0·87901 ± 0·00767
Scheeren: Meropoditenlänge ...	0·75447 ± 0·01453	0·78895 ± 0·01276
Scheeren: Carpopoditenlänge ...	0·69750 ± 0·01732	0·69895 ± 0·01725
Scheeren: Propoditenlänge ...	0·47333 ± 0·02617	0·54861 ± 0·02357

Beim Vergleich der Bestimmungswerthe der Differenzreihen ergiebt sich Folgendes:

TABELLE III.

Differenzreihen.

R, L = rechtshändige resp. linkshändige Thiere. D = Differenzen.

	Laterale Panzerränder (M)		Meropoditenlänge d. 1. Gangbeins (G)		Meropoditenlänge d. Scheeren (Ch)		Carpopoditenlänge d. Scheeren (C)		Propoditenlänge der Scheeren (P)	
	D		D		D		D		D	
	R	L	R	L	R	L	R	L	R	L
A	0·91000	0·83500	0·91750	1·15500	6·41750	6·67500	8·14000	7·78000	13·01750	12·55000
σ	0·49689	0·49272	0·55290	0·71132	1·06216	1·07674	1·15126	1·03759	1·70065	1·57560
β_3	0·06026	0·03896	−0·02236	−0·23337	−0·34074	−0·16845	0·32505	0·03241	− 0·60675	− 0·48127
β_4	5·99735	7·51097	4·48052	5·26774	3·71957	3·57525	3·88292	3·75459	4·52343	4·31115
Asymmetrie-Index	0·83770	0·79263	0·81320	0·87238	1·00000	1·00000	1·00000	1·00000	1·00000	1·00000

Die Durchschnittswerthe der Differenzreihen überwiegen bei den Rechtshändern in allen Fällen mit Ausnahme der Meropoditenlängen des Scheeren- und des zweiten Beinpaares. Da alle gemessenen Dimensionen auf der Seite der Kampfscheere die grösseren Durchschnittswerthe ergeben, so sind sie stets positiv.

Ihre Variabilitätsindizes verhalten sich bei links- und rechtshändigen Thieren wie die Durchschnittswerthe.

Die dritten Momentquotienten sind positiv für M und C, negativ für G, Ch und P. Ihrem absoluten Zahlenwerth nach sind sie überall bei den rechtshändigen Thieren grösser, ausser für G. Sie sind meistens kleiner, als die korrespondierenden Werthe der Einzelmerkmale.

Die vierten Momentquotienten sind für die drei Paare der Scheerendimensionen grösser bei den rechts-, für die beiden anderen Merkmalpaare bei den linkshändigen Thieren, und stets grösser als die korrespondierenden Werthe der Einzelmerkmale.

Die Asymmetrieindizes betragen für die drei paarigen Scheerendimensionen in Folge ihrer nahezu oder vollkommen auseinander fallenden Variationsgebiete stets Eins; die Kollektiv-Asymmetrie dieser Merkmalpaare ist demnach vollständig. Für die Lateralränder und die Meropoditen des zweiten Beinpaares ergeben sich echte Bruchwerthe, die bei Rechts- und Linkshändern etwas verschieden ausfallen.

Die Symmetrieverhältnisse der einzelnen Merkmalpaare werden durch das Wachsthum der Thiere derart beeinflusst, dass die Differenzen der bilateralhomologen Merkmale mit zunehmendem Alter an Grösse zunehmen. Die paarigen Merkmale wachsen also ungleich rasch, je nachdem sie sich auf der Seite der Fress- oder der Kampfscheere befinden, und zwar schneller auf der Seite der letzteren. Es muss daher zwischen den absoluten Differenzreihen positive Alterskorrelation bestehen.

Untersucht man die *Abhängigkeit der Kollektiv-Asymmetrie* der unvollständig asymmetrischen Merkmalpaare M und G von der hier als primär betrachteten Asymmetrie der Scheerenentwicklung, nämlich der Rechts- und Linkshändigkeit, nach dem von Pearson ([3.] pp. 435—436) für nicht numerische Merkmale angegebenen Verfahren*, so erhält man

$$\text{für } M \qquad \rho = 0{\cdot}95933 \pm 0{\cdot}00269$$
$$\text{„ } G \qquad \rho = 0{\cdot}97302 \pm 0{\cdot}00180$$

also nahezu vollkommene Abhängigkeit.

Für die Merkmalpaare mit vollständiger Asymmetrie ist natürlich auch diese Abhängigkeit eine vollkommene; man findet für sie stets den Werth $\rho = 1$.

Zum Vergleich füge ich die bisher unveröffentlichten korrespondierenden Werthe für paarige Merkmale zweier anderer asymmetrisch differenzierter Thierarten hier bei:

* Rechnungsbeispiel: $D(M)$. Cf. Anhangstabelle.

D:	−4	−3	−2	−1	0	1	2	3	Σ
f L	1	0	14	303	81	1			400
f R				1	63	310	23	3	400
Σ (L+R)	1	0	14	304	144	311	23	3	800

	−4 bis C	C bis 3	Σ
L	363·56	36·44	400
R	36·44	363·56	400
Σ	400	400	800

$$C = -0{\cdot}5 + \frac{81}{144} = 0{\cdot}06250 \qquad \rho = \sin 360° \cdot \frac{163{\cdot}56}{800} = 0{\cdot}95933.$$

a. *Pleuronectes flesus* L. 1060 rechts- und 60 linksäugige (♂ + ♀) Individuen.

	ρ	α R	α L
Gesammtzahl der Brustflossenstrahlen	0·80530	0·60443	− 0·58333
Zahl der Brustflossen-Theilstrahlen	0·99782	0·97778	− 0·98305
Gesammtzahl der Bauchflossenstrahlen	0·07811	0·01957	− 0·08333
Zahl der Bauchflossen-Theilstrahlen	0·54902	0·32600	− 0·37424
Endigungsstelle der Supraoccipitaläste der Seitenlinien	0·34170	0·12403	− 0·32305

b. *Eriphia spinifrons* Herbst. 694 rechts- und 255 linkshändige ♂.
544 „ „ 206 „ ♀.

	ρ ♂	ρ ♀
Zahl der Anterolateraldornen	0·01257	0·01885
„ „ Infraorbitaldornen	0·07533	0·10661
„ „ Facialdornen	− 0·01571	− 0·01571
„ „ Frontaldornen	0·05338	0·09411
„ „ Suprafrontaldornen	0·04711	0·00940

Die Asymmetrieindizes dieser Merkmalpaare liegen sämmtlich zwischen + 0·1 und − 0·1.

Aus den unter *a* und *b* aufgeführten Werthen ergiebt sich, dass die Kollektiv-Asymmetrie verschiedener bilateral-homologer Merkmalpaare von der jeweils als primär betrachteten bilateralen Differenzierung in ausserordentlich ungleichem Maasse abhängig ist, ferner, dass der Grad dieser Abhängigkeit bei unvollständiger Kollektiv-Asymmetrie eines Merkmalpaares zwar im allgemeinen konform, jedoch nicht proportional dem Grade der letzteren (dem Asymmetrieindex) zunimmt.

Die gegenseitige Abhängigkeit der individuellen Symmetrieverhältnisse der verschiedenen Paare bilateral-homologer Merkmale von einander ergiebt sich aus den korrelativen Beziehungen ihrer Differenzreihen. Hinsichtlich letzterer sind drei einander ausschliessende Möglichkeiten denkbar:

1. Mit überdurchschnittlicher Asymmetrie eines Merkmalpaares ist überdurchschnittliche eines anderen individuell verbunden und vice versa. Dies Verhalten würde seinen Ausdruck in positiver Korrelation der Differenzreihen finden.

2. Mit überdurchschnittlicher Asymmetrie eines Merkmalpaares ist unterdurchschnittliche eines anderen verbunden und umgekehrt. Individuelle Asymmetrien verschiedener Merkmalpaare gleichen sich gegenseitig aus. Hierbei würde negative Korrelation der Differenzreihen bestehen.

3. Der individuelle Grad der Asymmetrie eines Merkmalpaares ist unabhängig von demjenigen des anderen. Es besteht keine Korrelation zwischen ihren Differenzreihen.

Die wenigen, ausschliesslich von mir angestellten Untersuchungen an verschiedenartigem Material ergaben bisher übereinstimmend auffällig niedrige Korrelationskoeffizienten der Differenzreihen bilateral-homologer Merkmalpaare.

1. *Acerina cernua* L. (692 ♀).

	ρ_D	
Seitliche Kopf- und Mandibellängen in Procenten der Totallänge	0·10775	± 0·02536

2. *Pleuronectes flesus* L. (1060 rechtsäugige ♂ + ♀).

Gesammt- und Theilstrahlzahlen der Brustflossen	0·11104	± 0·02092
" " " " Bauchflossen	0·01330	± 0·02077
Gesammtstrahlzahlen der Brust- und der Bauchflossen	0·01359	± 0·02076
Theilstrahlzahlen der Brust- und der Bauchflossen	− 0·04125	± 0·02121
Gesammtstrahlzahlen der Brust- und Theilstrahlzahlen der Bauchflossen	0·07154	± 0·02068
Theilstrahlzahlen der Brust- und Gesammtstrahlzahlen der Bauchflossen	− 0·03568	± 0·02120

3. *Eriphia spinifrons* Herbst (Rechtshänder; 694 ♂ und 544 ♀).

Differenzreihen der beiderseitigen Dornzahlen der Anterolateral- und der Infraorbitalränder	♂:	− 0·00024	± 0·02583
	♀:	0·00345	± 0·02911
der Infraorbital- und der Frontalränder	♂:	0·04880	± 0·02584
	♀:	0·08088	± 0·02908
der Frontalränder und der Suprafrontalleisten	♂:	0·00966	± 0·02583
	♀:	− 0·06765	± 0·02897

Somit besteht bezüglich dieser Merkmalpaare, die mit Ausnahme der beiden ersten (*Acerina*) keinen wesentlichen Altersveränderungen ausgesetzt sind, nur sehr geringe oder—in den weitaus meisten Fällen—keine mit Sicherheit nachweisbare Korrelation ihrer Differenzreihen, d. h. die individuellen Symmetrieverhältnisse der verschiedenen bilateral-homologen Merkmalpaare sind von einander unabhängig*.

* Durch Entwicklung des Ausdrucks

$$(a)\quad \rho_D = \frac{\Sigma\,(\chi_{DI}\,\chi_{DII})}{n\sigma_{DI}\,\sigma_{DII}} = \frac{\Sigma\,(\chi_d - \chi_s)_I\,(\chi_d - \chi_s)_{II}}{n\sigma_{DI}\,\sigma_{DII}}$$

erhält man

$$(b)\quad \rho_D = \frac{\rho_{a1a11}\sigma_{d1}\sigma_{d11} - \rho_{a1s11}\,\sigma_{d1}\sigma_{s11} - \rho_{s1a11}\,\sigma_{s1}\sigma_{d11} + \rho_{s1s11}\sigma_{s1}\sigma_{s11}}{\sqrt{(\sigma_d^2 + \sigma_s^2 - 2\rho\sigma_d\sigma_s)_I \cdot (\sigma_d^2 + \sigma_s^2 - 2\rho\sigma_d\sigma_s)_{II}}},$$

wobei *I* und *II* die Merkmalpaare, deren Differenzreihen kombiniert sind, bezeichnen. Dieser Ausdruck ergiebt zunächst dann von Null abweichende (positive oder negative) Werthe, wenn die Variabilität der Merkmale beider Paare beträchtlich auf den beiden Körperseiten differiert. Ist die Variabilität der homologen Merkmale auf beiden Körperseiten gleich, so reduziert sich obiger Ausdruck auf die Form

$$(c)\quad \rho_D = \frac{\rho_{a1a11} - \rho_{a1s11} - \rho_{s1a11} + \rho_{s1s11}}{\sqrt{(1-\rho_I)\,(1-\rho_{II})}}$$

Bei dem vorliegenden Material ist nun von vorn herein stärkere Korrelation zwischen den Differenzreihen deshalb zu erwarten, weil die individuellen Differenzen der paarigen Merkmale mit der Grössenzunahme der Thiere wachsen. Ich habe diesen Umstand einstweilen nur an zwei Kombinationen solcher Merkmalpaare geprüft, deren Beziehungen ein besonderes Interesse boten. Die eine derselben enthält die metamer-homologen Meropoditenlängen der Scheeren und der vorderen Schreitbeine (*Ch* und *G*), die andere die Merkmalpaare stärkster Asymmetrie (*C* und *P*). Ausser den Korrelationskoeffizienten der Differenzreihen (ρ_D) wurden auch diejenigen der Einzelmerkmale ermittelt.

TABELLE IV.

	R		*L*	
	Chs	*Chd*	*Chs*	*Chd*
Gs	0·80217 ±0·01202	0·82526 ±0·01076	0·84841 ±0·00948	0·79955 ±0·01217
Gd	0·79660 ±0·01182	0·84257 ±0·00978	0·83269 ±0·01037	0·80305 ±0·01198
ρ_D	0·17358 ± 0·03721		0·18654 ± 0·03255	
	Cs	*Cd*	*Cs*	*Cd*
Ps	0·61676 ±0·02090	0·56311 ±0·02303	0·83941 ±0·00985	0·63589 ±0·02009
Pd	0·59847 ±0·02162	0·83549 ±0·01018	0·61757 ±0·02080	0·64632 ±0·01964
ρ_D	0·71636 ± 0·01715		0·67041 ± 0·01857	

Die Kollektiv-Asymmetrie des untersuchten Materials findet auch in dem Verhalten der zusammengehörigen Tetraden von Korrelationskoeffizienten der nicht homologen paarigen Einzelmerkmale ihren Ausdruck. Bei Symmetrie sind in der Regel die Korrelationskoeffizienten von derartigen Merkmalen derselben Körperseite einander gleich und meistens höher als die von solchen entgegengesetzter Körperseiten, welche ihrerseits wiederum gleich sind. Im vorliegenden

und ergiebt merkliche Werthe nur dann, wenn ein Unterschied der korrelativen Beziehungen zwischen den nicht homologen Merkmalen derselben und den nicht homologen Merkmalen entgegengesetzter Körperseiten besteht.

Nach Formel (*b*) finde ich für ρ_D unserer Beispiele

	G : *Ch*	*C* : *P*
R	0·17360	0·71636
L	0·18656	0·67041.

Die Korrelation des ersten Falles wird wesentlich durch den Unterschied der Variabilität der homologen Einzelmerkmale auf den beiden Körperseiten, die des zweiten sowohl hierdurch, als auch durch die Verschiedenheit der korrelativen Beziehungen der nicht homologen Einzelmerkmale bedingt.

Falle finden wir zwar, dass die höchste Korrelation zwischen den Merkmalen der Kampfscheerenseite besteht, dass aber diejenige zwischen den Merkmalen der Seite der Fressscheere nicht oder kaum höher ist, als die zwischen Merkmalen entgegengesetzter Körperseiten. Die beiden Paare metamer-homologer Merkmale stehen in engerer Korrelation, als die einander unmittelbar benachbarten Paare nicht-homologer Dimensionen der Scheerenglieder.

Das Gesammtresultat unserer Untersuchungen der Symmetrieverhältnisse der verschiedenen bilateral-homologen Merkmalpaare von *Gelasimus pugilator* lässt sich etwa folgendermaassen ausdrücken:

Die Kollektiv-Asymmetrie der einzelnen bilateral-homologen Merkmalpaare, welche ihren Ausdruck in den Asymmetrieindizes findet, hängt de facto gänzlich von der als primär betrachteten, als "Rechts-" oder "Linkshändigkeit" bezeichneten Differenzierung der durch die Medianebene getrennten Körperhälften ab. Trotzdem stehen die individuellen Unterschiede der einzelnen Merkmalpaare in nur schwacher oder in mittlerer Korrelation zu einander.

Demnach entwickeln sich die untersuchten bilateral-homologen Merkmale auf den beiden seitlichen Körperhälften in hohem Grade verschieden. Dies ist jedoch nicht die Folge eines die beiden individuellen Körperhälften gemeinschaftlich in dem Sinne beeinflussenden Prozesses, dass die Grösse der Unterschiede eines Merkmalpaares diejenige von solchen anderer reguliert, denn die individuellen Symmetrieverhältnisse der einzelnen Merkmalpaare sind ja von einander entweder unabhängig oder in nur mässigem Grade abhängig. Kollektiv-Symmetrie oder -Asymmetrie ist die Folge grösserer oder geringerer Aehnlichkeit des Entwicklungsganges der beiden homologen Körperhälften, deren einzelne Merkmale individuell variabel sind. Je ähnlicher die Variationsreihen der homologen Merkmale, je höher die gewöhnlich zwischen ihnen bestehende, positive Korrelation, desto grösser allerdings die Wahrscheinlichkeit, hinsichtlich ihrer vollkommen symmetrische Individuen anzutreffen. Doch steht die Grösse des individuellen Unterschiedes eines Merkmalpaares für gewöhnlich überhaupt nicht im Zusammenhang mit der eines anderen, und auch bei dem vorliegenden Material nur mittelbar, auf Grund besonderer mechanischer und trophischer Bedingungen.

Zum Schlusse möchte ich nicht verfehlen, Herrn Robert M. Yerkes auch an dieser Stelle meinen verbindlichen Dank für die liebenswürdige Bereitwilligkeit auszusprechen, mit der er mir sein interessantes Material zur Benutzung überliess.

LITTERATUR.

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2. R. M. Yerkes. A Study of Variation in the Fiddler-Crab (*Gelasimus pugilator* Latr.). Proc. Amer. Acad. Arts Sc. Vol. XXXVI. pp. 417—422. (Contrib. Zool. Lab. Mus. Comp. Zool. Harvard Coll. No. 119.)
3. K. Pearson. The Grammar of Science. 2nd ed. London, 1900.

Zusammenfassung.

1. Bei den Männchen der *Gelasimus*-Arten besteht eine ausgeprägte Differenzierung der beiden Scheeren nach Form und Grösse. Die grössere (Kampf-) Scheere kann der rechten oder der linken Körperseite angehören.

2. Die Untersuchungen von Yerkes an männlichen *Gelasimus pugilator* Latr. ergaben ungleiche Grössenverhältnisse nicht nur der korrespondierenden Scheerenglieder beiderseits, sondern auch der Lateralränder des Cephalothorax und der Meropoditen des zweiten Beinpaares, derart, dass sämmtliche bilateral-homologen Dimensionen im Durchschnitt auf der Seite der Kampfscheere stets grösser als auf der Gegenseite sind.

3. Die Variabilität bilateral-homologer Dimensionen überwiegt auf der Seite der Kampfscheere.

4. Die Differenz zweier bilateral-homologer Dimensionen nimmt mit steigender Totallänge zu; es findet rascheres Wachsthum der auf der Seite der Kampfscheere befindlichen Organe statt.

5. Der wie bei bilateral-homologen Merkmalen überhaupt stets positive Korrelationskoeffizient der untersuchten Paare homologer Dimensionen ist um so grösser, je näher die gemessenen Organe einander liegen.

6. Die Scheerendimensionen verhalten sich vollständig, die übrigen zwar stark, aber unvollständig asymmetrisch. Erstere sind also ausnahmslos auf der Seite der Kampfscheere grösser als auf der der Fressscheere, während sich bezüglich letzterer vereinzelt auch symmetrische oder gegensätzlich asymmetrische Individuen finden.

7. Die Abhängigkeit der geschilderten Ungleichheiten der bilateral-homologen Merkmale von der Stellung der beiden Scheeren zu den Körperseiten (Rechts- und Linkshändigkeit) entspricht ihren Asymmetrieindizes. Sie ist nahezu vollständig bezüglich der Lateralränder und der Meropoditenlängen des zweiten Beinpaares, absolut bezüglich der bilateral-homologen Scheerendimensionen. Die Kollektiv-Asymmetrie der Formengemeinschaft ist demnach hinsichtlich der untersuchten Merkmalpaare so gut wie vollkommen.

8. Die Differenzreihen ergeben, da sie nach (4) in Wachsthumskorrelation stehen, bei dem vorliegenden Material höhere Korrelationskoeffizienten, als bei früheren Beobachtungen. Doch ist an den beiden einstweilen untersuchten Kombinationen derselben die Zunahme der Korrelationskoeffizienten nicht sehr bedeutend; insbesondere stehen trotz ihrer die individuellen Unterschiede der Meropoditenlängen des ersten und des zweiten Beinpaares in bemerkenswerth niedriger Korrelation.

9. Das Bestehen von Korrelation in den sub (8) genannten Fällen bildet eine Ausnahme von der sonst geltenden Regel, dass die individuellen Verschiedenheiten eines bilateral-homologen Merkmalpaares ihrer Grösse nach gänzlich

unabhängig von denen eines anderen erscheinen. Sie erklärt sich zum Theil durch Wachsthumskorrelation, zum Theil ist sie wahrscheinlich die Folge der ungleichen mechanischen und trophischen Bedingungen, welchen die paarigen Organe auf Grund der ausserordentlichen Grössendifferenzierung der beiden Scheerenbeine unterliegen.

10. Sind nun im vorliegenden Falle die Differenzen der verschiedenen bilateralhomologen Merkmalpaare auch nicht gänzlich unabhängig von einander, so genügt die Intensität ihrer korrelativen Beziehungen doch bei weitem nicht zur Erklärung ihrer nahezu resp. durchaus vollkommenen Kollektiv-Asymmetrie. In dieser Beziehung schliessen sich also die hier erhaltenen Befunde denen an, in welchen die individuellen Differenzen verschiedener paariger Merkmale überhaupt keine Abhängigkeit von einander aufweisen.

ANHANGSTABELLE.

Differenzreihen ($u = 0{\cdot}5$ mm.).

Differenzen		*−2*	*−1*	*0*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*
Lateralränder des Cephalothorax ...	*R*	—	1	63	310	23	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	L	—	1	81	303	14	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Meropoditenlängen d. 1. Gangbeinpaares	*R*	—	2	71	287	38	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	L	2	4	39	252	91	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chelare Meropoditenlängen	*R*	—	—	—	—	1	2	12	52	140	140	46	7	—	—	—	—	—	—	—	—	—
	L	—	—	—	—	—	2	8	38	119	150	72	8	3	—	—	—	—	—	—	—	—
Chelare Carpopoditenlängen	*R*	—	—	—	—	—	—	—	4	20	82	162	87	35	8	1	1	—	—	—	—	—
	L	—	—	—	—	—	—	1	4	33	113	161	72	14	1	1	—	—	—	—	—	—
Chelare Propoditenlängen	*R*	—	—	—	—	—	—	—	—	2	0	3	11	13	31	65	118	100	31	21	4	1
	L	—	—	—	—	—	—	—	—	2	1	3	10	27	44	88	133	53	29	9	1	—

VARIATION AND CORRELATION IN ARCELLA*.

By RAYMOND PEARL and FRANCES J. DUNBAR.

I. Introduction.

The purpose of this paper is to present the results of a quantitative study of the variability of the common shelled rhizopod, *Arcella vulgaris*. Comparatively little is known regarding the amount of the individual variation which exists in the different groups of the Protozoa, and it seems highly desirable that our knowledge in this field should be extended. Almost the only piece of quantitative work on the variability of these forms which has appeared is that of Simpson† on *Paramœcium*. It was with the idea of determining the variation in a still lower form than *Paramœcium* that the present work was undertaken. The plan followed in this work was, however, somewhat different from that of Simpson. Since his primary purpose was the determination of the amount of variation following binary fission, only organisms of known immediate ancestry were measured. The labour involved in isolating a particular *Paramœcium* undergoing division, and in measuring the daughter individuals after fission has been completed, is very considerable, and consequently it is not surprising that measurements for but 100 pairs were collected.

Our plan was to determine the amount of variation in a representative sample of a homogeneous population of *Arcellae*, without reference to the immediate ancestry of the individuals of the sample. This is the course which not only usually is, but in most cases must be, followed in studying the variation in higher forms, since the difficulties of getting a sufficiently large number for statistical purposes of individuals of known ancestry are very great. By working in this way it would seem that we might get values of the variation coefficients which would be better for the purposes of comparing protozoan with metazoan variability than those of Simpson. The practical difficulties in handling the material in this way

* Contributions from the Zoological Laboratory of the University of Michigan.

† Simpson, J. Y., "The Relation of Binary Fission to Variation." *Biometrika*, Vol. I., pp. 400—404, 1902.

are of course very greatly reduced, and consequently it becomes possible to measure a large series of individuals.

Besides the determination of the constants of the simple variation in single dimensions we also wished to ascertain the amount of the correlation in the variation of different parts. As in the case of simple variation Simpson's is the only work which we have on correlation in any protozoan. His data enabled him to determine, in addition to the correlation between the two individuals of the divided pair, the correlation between length and breadth of the same individual. His value for the length-breadth correlation in the same individual was ·421. It is very important to determine whether there exists in general a higher, or lower, or equal amount of correlation between the parts of lower organisms as compared with higher. This question of the relative amount of correlation in different forms becomes very significant when any attempt is made to solve the more general problem of the physiological basis of the phenomenon of correlation in variation*. Although the fundamental character of this general problem is apparent, yet comparatively little has been done towards solving it. It seems not unlikely that the ultimate method of attacking this problem will be by means of experiment, but some light can certainly be thrown on the question by determining the amount of correlation in variation in different groups of organisms. Such determinations can then be used as a definite quantitative basis, from which to proceed by experimental methods. It has seemed to one of the writers that one good starting point for the investigation of this problem would be a thorough study of variation and correlation in the cell, including both free-living and tissue cells. The present paper forms our first contribution to this study.

II. Material and Methods.

The form used in this work was the common *Arcella, A. vulgaris.* A very complete description of this organism, illustrated with coloured figures, is given by Leidy†. It is also fully described by Bütschli‡.

Arcella is so generally distributed and well known an organism as to make only a very brief account of its taxonomic position, structure, etc., necessary here. *Arcella* is a shelled rhizopod belonging to the group *Imperforata*, family *Arcellina*, as defined by Bütschli. The shell is composed of chitinous material, and varies in colour from almost purely colourless transparency to a deep brown. In surface view the shell is seen to be composed of very small hexagonal elements packed closely together. The normal *Arcella* shell is circular in outline, with an

* For an historical account of the discussion of the phenomenon of correlation by earlier workers cf. Radl, E., "Ueber die Bedeutung des Prinzips von der Korrelation in der Biologie." *Biol. Centralbl.*, Bd. xxi. pp. 401–416, 491–497, 550–560, 585–591, 605–621, 1901.

† Leidy, J., "Freshwater Rhizopods of North America." *Rep. U. S. Geol. Surv. of the Territories* (Hayden). Vol. xii. 1879, pp. 166–173. Plate XXVII.

‡ Bütschli, O., "Protozoa," in Bronn's *Klassen und Ordnungen des Thierreiches.* Bd. i. 1 Abth. 1880–82.

approximately plane ventral surface, containing in its centre the circular "mouth" opening. The form of the shell is shown in side view in Fig. 1.

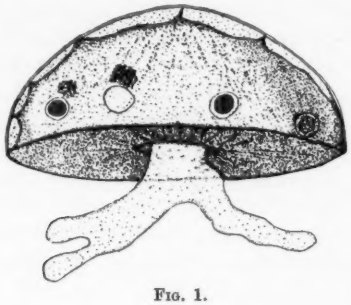

FIG. 1.

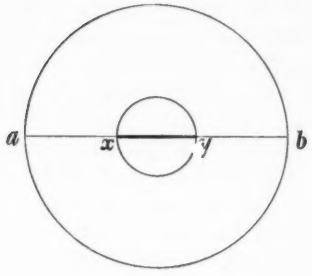

FIG. 2.

The points studied in the work were: (i) the variation of the diameter of the shell (Fig. 2, *ab*), (ii) the variation in the diameter of the "mouth" opening (Fig. 2, *xy*), (iii) the variation in colour, and (iv) the correlation between (i) and (ii), and (i) and (iii). For verbal convenience we shall refer throughout the paper to character (i) (the total diameter of the shell) as the *outer* diameter, and to character (ii) (the diameter of the "mouth" opening) as the *inner* diameter.

The measurements of the outer and inner diameters were made in the following way. At the beginning of the taking of the series of measurements a compound microscope with a camera lucida attached was set up in a certain place in the laboratory and adjusted so that both microscope and camera gave optically their best results. The arrangement was then left undisturbed*. The amount of magnification obtained by the use of microscope and camera with the paper at the level of the table was then very carefully measured several times and the mean of all these observations used as the true value of the magnification.

* Except once during the course of the measuring, when it became necessary to use the microscope elsewhere. When replaced it was adjusted so as to be in the same condition as before the removal.

The *Arcellae* were then taken with a pipette from the culture dish and placed a few at a time on a slide in water, and covered with a cover-slip. Then with a sharp needle the points marking the limits of the maximum diameter of the shell and of the "mouth" opening as seen in the camera image were pricked on a card of smooth drawing-paper laid on the table under the mirror of the camera. After the size of all the *Arcellae* on a slide had been pricked in this way, the slide was cleaned off and a fresh lot of individuals taken from the culture.

In this way cards were obtained bearing the dimensions magnified approximately 400 times, and marked by needle pricks. These dimensions on the cards were then measured by means of a sliding arm calliper, bearing a vernier reading to fiftieths of a millimeter. The measurements so obtained were divided by the magnification of the microscope-camera combination and reduced to mikrons. The measurements in mikrons were then permanently recorded.

From a series of test measurements (50 in number) of distances of known size (spaces of a net micrometer) made by this method we were led to the conclusion that microscopical measurements made in this way were very accurate. In fact we are inclined to believe that microscopical measurements may be made more accurately and, considering the accuracy, more expeditiously, than in any other way except by the use of a filar ocular micrometer, which unfortunately was not available for this work.

A point which needs consideration in connection with the method of making measurements is the question of symmetry of the shells. While it is known as a matter of common observation that *Arcella* shells are in general circular in outline, it is not so certain whether they are all exactly circular. We found in examining a large number of shells that there are a considerable number which are not exactly circular but are slightly ovate in outline. With practice an observer becomes very skilful in detecting any deviation from the circular outline, and in taking our measurements whenever it was suspected that any such deviation was present in a shell two pairs of diameters (inner and outer) at right angles to one another were measured instead of a single pair. These diameters were so taken as to be, as nearly as one could judge, the maximum and minimum diameters. Then the average of the two was taken as representing what the diameter of this shell would be were it symmetrical. All these deviations observed were small—in most cases extremely small. No strikingly asymmetrical shells were found in the course of this work.

In taking the individuals for measurement there was no selective choice exercised. Some water was drawn up from the culture in a pipette and dropped on a slide. If there were any *Arcellae* in the water they were all measured. If none were found a new sample of water was taken. The sample of the population measured was a "random sample."

In order to test quantitatively the generally accepted view that there is a considerable degree of correlation between darkness of colour and size in *Arcella* shells it was desired to collect statistical data on the colour of the shells. The

problem of recording definitely the colour of such an organism as *Arcella* is a very difficult one. After trying and abandoning several methods of recording colour we finally decided upon the following as sufficiently accurate for our purpose. In the work of Leidy already referred to, Plate XXVII contains a number of figures of colour varieties of *Arcella*. These figures are extremely well chosen to typify the different colour classes, ranging all the way from colourless transparency to a very deep brown. For our colour determinations we chose four of these figures on this Plate as types with which to compare the colour of the *Arcellae* observed. As typical of the lightest shells we took Fig. 14, and called this our colour type *A*. The colour of this figure on the Plate is a very light yellow-brown. It very well represents the colour of the lightest shells we found. For the next darker type we chose Fig. 7, and designated this as colour type *B*. Shells falling within this type have a distinct yellow-brown colour, and yet are still fairly transparent. Fig. 19 served as our colour type *C*. Shells falling in this colour class may be roughly described as of medium-brown colour, with a sensible though small admixture of yellow. As representative of the darkest individuals, our colour type *D*, we chose Leidy's Fig. 2. This is the colour most frequently observed in *Arcella* shells, and is a dark, even brown.

As the *Arcella* shells were measured their colour was compared with these figures and each shell was recorded as *A*, *B*, *C* or *D*, according to the figure which it most nearly matched. It was found in practice that the colour of the shells could be more accurately classified in this way than by comparing with sheets of coloured paper for example, because the thing with which the colour was compared in this method was an actual representation of an *Arcella*. While the method gives us no quantitative determination of the amount of pigmentation it does furnish a reasonably good classification of *Arcella* shells by colour, which can be used for purposes of correlation. This was all we hoped or desired to get in the present work.

The 504 individuals of which measurements were made were all taken from a single small laboratory culture dish. The material was collected from a small lake in the vicinity of Ann Arbor, and the few *Arcellae* originally in the collection multiplied rapidly under the conditions of the laboratory culture*. At the time when the measurements were begun the *Arcellae* were very abundant. Since the individuals were all taken from one small culture dish they may be considered a very homogeneous sample of this *Arcellae* population, as far as environmental conditions are concerned. The sample is not, however, quite homogeneous with respect to age, for the following reasons. Pressure of other work made it necessary for us to extend the time of making measurements over a period of about three weeks. It is likely that some of the last individuals to be measured represented later generations than those to which those measured earlier belonged. That this was the case is indicated by the form of the frequency polygons obtained. It will be shown farther on in the paper, however, that there was on the whole no sensible increase in size of the shells during the time which the making of the measurements covered.

* [Since the original *Arcellae* were *few* in number, it should be noted that the authors are dealing rather with a few large "fraternities" than a general population of *Arcellae*; such, however, is probably the constitution of most "cultures." ED.]

What we have then as material for this biometrical study is a random sample of the individuals of a population of *Arcella*, covering a period of about three weeks in the life of the culture. It may be considered that we have a section three weeks long in the cultural history, and have investigated the conditions of the individual *Arcellae* falling within that section.

III. Results.

A. *Variation in Outer and Inner Diameters.*

The results of the measurements of the outer and inner diameters of 504 individuals are shown in Tables I and II.

TABLE I.

Outer Diameter. Class unit = 2 mikrons.

Diameter of shell in mikrons	Frequency	Diameter of shell in mikrons	Frequency
42—44	1	*70—72*	2
44—46	2	*72—74*	2
46—48	—	*74—76*	3
48—50	5	*76—78*	3
50—52	22	*78—80*	4
52—54	147	*80—82*	2
54—56	210	*82—84*	—
56—58	70	*84—86*	1
58—60	13	*86—88*	1
60—62	1	*88—90*	1
62—64	5	*90—92*	—
64—66	1	*92—94*	1
66—68	3	*94—96*	1
68—70	3		
		Total ...	504

TABLE II.

Inner Diameter. Class unit = 1 mikron.

Diameter of shell in mikrons	Frequency	Diameter of shell in mikrons	Frequency
11—12	4	*23—24*	3
12—13	5	*24—25*	2
13—14	25	*25—26*	2
14—15	101	*26—27*	1
15—16	189	*27—28*	—
16—17	120	*28—29*	—
17—18	29	*29—30*	1
18—19	4	*30—39*	—
19—20	7	*39—40*	1
20—21	3		
21—22	4		
22—23	3	Total ...	504

For these frequency distributions the following constants have been determined: mean, median, mode, standard deviation, coefficient of variation, together with the probable errors of the three most important constants, the mean, the standard deviation and the coefficient of variation. Only an approximate value of the mode was obtained, the method used being that described by Yule*, wherein an approximation to the value of the mode is determined from the relation: Mode = Mean − 3 × (Mean − Median)†. In determining the value of the standard deviation from the equation, $\sigma = \sqrt{\mu_2}$, Sheppard's correction was used in obtaining μ_2. The formula used in determining the probable error of the coefficient of variation was that given by Macdonell‡ after Pearson, viz., P. E. of $v = \pm .6745 \frac{v}{\sqrt{2n}} \left[1 + 2\left(\frac{v}{100}\right)^2\right]^{\frac{1}{2}}$ where v is the coefficient of variation, and n is the number of individuals.

The values of these constants for the frequency distributions of variation in the outer and inner diameters are given in Table III.

TABLE III.

Constants for Size Variations in 504 Individuals of Arcella vulgaris.

	Outer diameter	Inner diameter
Mean	55·7897 ± ·1721 mikrons	15·9107 ± ·0653 mikrons
Mode	52·5635 ,,	15·0357 ,,
Median	54·7143 ,,	15·6190 ,,
Standard Deviation ...	5·7283 ± ·1217 ,,	2·1731 ± ·0462 ,,
Coefficient of Variation	10·2676 ± ·2204 %	13·6578 ± ·2955 %

Discussion of Results.

There are several points brought out by these constants regarding variation in *Arcella*, which seem to need some further discussion.

Taking first the constants defining the type of the species with respect to the characters under consideration, it is seen that the mean and the mode are separated by an appreciable distance, or in other words the distribution is skew. In the case of the outer diameter this distance amounts to 3·226 mikrons, or 1·61 abscissal units. In the case of the inner diameter the distance between mean and mode is ·875 mikrons, or approximately ·88 of the abscissal unit for this distribution. From these absolute values of the differences it would appear that the distribution for the outer diameter was markedly more skew than the distribution for the inner diameter. It is to be remembered however that the means and class units

* Yule, G. U., "Supplementary Note on the Determination of the Mode." *Jour. Roy. Stat. Soc.* Vol. LIX. p. 398.

† *Phil. Trans.* Vol. 186, A, p. 375.

‡ *Biometrika*, Vol. I. p. 189.

in the two cases are different. If we compare, instead of the absolute, the relative differences, by taking the percentages of the differences between mean and mode in the respective means, we reach the following results: the percentage difference between the mean outer diameter and the modal outer diameter in the mean outer diameter is 5·78 °/₀. The percentage difference between the mean inner diameter and the modal inner diameter in the mean inner diameter is 5·49 °/₀. These relative values are in close accord and lead to the same conclusion regarding the relative skewness of the two curves as that reached by mere inspection, namely, that the two distributions are very closely alike in their form. We would suggest this method just described of taking the percentage difference between the mean and the mode as a useful rough method of comparing the relative skewness of frequency distributions, in cases where it is not feasible to compute the skewness exactly from the moments*.

From the mean values for the two diameters it is seen that the whole diameter of the shell (outer) is on the average approximately 3·5 times the diameter of the "mouth" opening (inner). More exact relations between these two dimensions will be given later in the paper in the form of regression equations.

The coefficients of variation show clearly that the inner diameter is distinctly more variable than the outer. This relation is shown in Table IV.

TABLE IV.

Coefficients of Variation. Outer and Inner Diameters.

	Coefficient	Probable error of coefficient
Inner diameter	13·6578	·2955
Outer ,, ...	10·2676	·2204
Difference	3·3902	—
Probable error of difference	—	·3686

The difference is roughly ten times its probable error and hence may be considered significant.

These two frequency distributions furnish a good example of a case where the absolute concentration of variates given by the standard deviation cannot be used for the comparison of the relative variability of two characters in which the means are widely different. According to the standard deviations in the case under consideration the outer diameter would appear to be twice as variable as

[* Skewness has been defined as the ratio of the distance between mean and mode to the standard-deviation; we find for it in the above cases: ·5632 for outer, ·4027 for inner diameter distributions. These are considerable amounts and readily comparable with the values found in other cases. Ed.]

the inner, and in fact is, so far as absolute size of deviation is concerned. Taking the size of the deviations in relation to the respective means, however, as has been seen, we find the inner diameter to be significantly more variable than the outer.

It is of interest to compare the variability of *Arcella* with that of *Paramœcium* as determined by Simpson*. In his series of 100 *Paramœcia* the coefficient of variation for length was 8·361, and for breadth 13·439. The value of this coefficient for length is less than either of the coefficients for the characters of *Arcella* studied. The value of the coefficient of variation for the breadth of *Paramœcium* (13·439) is very nearly equal to that for the inner diameter of *Arcella* (13·658). Both the coefficients for *Paramœcium* are values of the same general order of magnitude as the coefficients for *Arcella*. From a comparative standpoint this result is of considerable interest. It is highly desirable that quantitative studies of the variation in other *Protozoa* reproducing primarily by the method of fission be made, in order to determine whether a value of approximately 10 % for the coefficient of variation is characteristic of variation in individuals produced by binary fission. The finding of such closely accordant values for the variation in two such widely different protozoan groups as the rhizopods and the holotrichous ciliates would seem to be of some significance. The senior author of this paper hopes to carry on some further investigations bearing on this problem, using other species of *Protozoa*.

It may again be noted in passing that in the sample of an *Arcella* population here studied we have a random general sample of a population produced by fission, the individuals not being chosen with reference to their immediate ancestry, as was the case in Simpson's work. It is interesting to find such close agreement in the values for the variation in samples collected in these different ways.

It is of some interest to compare the size of the *Arcellae* found in this study of a single culture with the values given by Leidy from the results of his studies of *Arcellae* from all parts of the country. Leidy says†: "The shell of *Arcella vulgaris* ranges from $\frac{1}{580}$ to $\frac{1}{165}$ of an inch in breadth, $\frac{1}{690}$ to $\frac{1}{350}$ of an inch in height, with the mouth $\frac{1}{2000}$ to $\frac{1}{520}$ of an inch in breadth, and elevated $\frac{1}{4100}$ to $\frac{1}{1500}$ of an inch." Reducing the values for "breadth of shell" (outer diameter), and "breadth of mouth" (inner diameter) to mikrons and comparing with our data, we get the following results.

Leidy's data { Range of breadth of shell: ca. 49—152 mikrons.
" " opening: ca. 12·7—49 mikrons.

Our data { Range of outer diameter: ca. 42—96 mikrons.
Range of inner " : ca. 11—40 " .

(With only one individual exceeding 30 mikrons in inner diameter.)

It is seen from this that the range observed by Leidy extends beyond ours only at the upper end.

* *Biometrika*, Vol. I. p. 405. † *Loc. cit.* p. 173.

B. *Variation in Colour.*

The colour determinations were made in the way already described (p. 325) for 371 individuals. The frequency distribution for colour is given in Table V.

TABLE V.

Frequency Distribution of Colour.

Colour class	Frequency
A	24
B	75
C	75
D	197
Total ...	371

Class *A* includes individuals of the lightest colour; class *D* the darkest individuals, and classes *B* and *C* intermediate gradations. As was expected the largest number of individuals fell in class *D*. A majority of all the individuals fall within this darkest colour class. The number of lighter coloured individuals is, however, larger than probably would have been predicted from general observation.

The correlation between colour and size will be discussed in a later section.

C. *Correlation.*

The correlations principally studied were those existing between the outer and inner diameters, and between the outer diameter and colour.

1. *Correlation between outer and inner diameters.*

The correlation table showing the relation between the total diameter of the shell and the diameter of the opening is exhibited in Table VI.

The value of the coefficient of correlation deduced from this table by the usual formula

$$r = \frac{S(xy)}{n\sigma_1\sigma_2}$$

is

$$r = \cdot 836 \pm \cdot 007.$$

A correlation coefficient of this magnitude of course indicates a high degree of correlation between the outer and inner diameters in *Arcella*. The value is considerably greater than that obtained by Simpson* for the correlation between the length and breadth of individual *Paramœcia*. His value for r in this case is

* *Loc. cit.* p. 403.

TABLE VI.

Correlation between Outer and Inner Diameters in Arcella.

Outer. Measurements in Mikrons.

Inner.	42—44	44—46	46—48	48—50	50—52	52—54	54—56	56—58	58—60	60—62	62—64	64—66	66—68	68—70	70—72	72—74	74—76	76—78	78—80	80—82	82—84	84—86	86—88	88—90	90—92	92—94	94—96	Totals
11—12	1	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
12—13	—	—	—	1	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
13—14	—	—	—	2	5	13	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25
14—15	—	—	—	1	8	38	42	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	101
15—16	—	—	—	1	5	68	92	20	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	189
16—17	—	—	—	—	1	23	60	30	3	—	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	1	—	120
17—18	—	—	—	—	1	2	12	7	4	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	29
18—19	—	—	—	—	—	—	—	—	2	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
19—20	—	—	—	—	—	—	—	—	1	—	3	—	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	7
20—21	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	1	—	—	—	—	—	—	—	—	3
21—22	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	2	—	—	—	—	—	—	—	—	—	—	4
22—23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—	3
23—24	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	3
24—25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	2
25—26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	2
26—27	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
27—28	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
28—29	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
29—30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1
30—39	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
39—40	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Totals	1	2	—	5	22	147	210	70	13	1	5	1	3	3	2	2	3	3	4	2	—	1	1	1	—	1	1	504

·421 ± ·055. The higher value for the correlation coefficient of the characters studied in the *Arcella* shell over the value for length and breadth of *Paramœcium* is what would perhaps be expected from general considerations regarding the two cases. The shell of *Arcella* is a very definitely formed, firm structure, which after its production is not easily changed in its shape by environmental changes. On the other hand the body of a *Paramœcium* is composed of soft, yielding protoplasm, bounded externally only by a thin, flexible pellicle. It is well known to every biologist that changes of form in the body of *Paramœcium* are very easily and quickly produced by changes in the surrounding conditions. In this event it would not be expected that there would be so close and definite a relationship between the dimensions of length and breadth in this form as exists between the two diameters of the firm, unyielding, and definitely formed shell of *Arcella**.

Passing now to the regression equations, we get from the usual equations for the regressions†

$$b_1 = r\frac{\sigma_1}{\sigma_2}$$

and

$$b_2 = r\frac{\sigma_2}{\sigma_1},$$

by substituting the values already obtained for r, σ_1, and σ_2, the following values for the regression coefficients between outer and inner diameters of *Arcella* shells,

$b_1 = 0{\cdot}317$ (regression of inner on outer diameter),

$b_2 = 2{\cdot}204$ („ „ outer „ inner „).

To express in words the significance of these equations we may say that: (1) the mean increase in the diameter of the opening in *Arcella* shells for every increase of 1 mikron in the whole diameter of the shell is ·317 mikrons; and (2) the mean increase in the total diameter of *Arcella* shells for every increase of 1 mikron in the opening is 2·204 mikrons.

The regression lines referred to the means as origin have the form:

$$x = {\cdot}317\, y,$$

$$y = 2{\cdot}204\, x.$$

In these equations x stands for deviations from the mean inner diameter, and y for deviations from the mean outer diameter. Reducing these to actual values instead of deviations by the method described by Yule‡, and letting D_i denote the

* We may also expect a difference from Simpson's value, because in the first place our correlation has not been corrected for growth, and in the second place two breadths expressing generally *size* are *a priori* more likely to be highly correlated than a length and breadth which also involve the factor of *shape*. Thus the length and breadth of the human skull for most races are less highly correlated than two breadths such as the frontal and bizygomatic breadths.

† Yule, G. U., "On the Theory of Correlation." *Jour. Roy. Stat. Soc.* Vol. LX. 1897, p. 818.

‡ *Loc. cit.* p. 827.

probable size in mikrons of the *inner diameter* and D_o the probable size in mikrons of the *outer diameter*, we get for the regression equations:

$$D_i - 15{\cdot}9107 = {\cdot}317\,(O - 55{\cdot}7897), \quad \text{or} \quad D_i = {\cdot}317\,O - 1{\cdot}775 \ \ldots\ldots\ldots\text{(i)},$$
$$D_o - 55{\cdot}7897 = 2{\cdot}204\,(I - 15{\cdot}9107), \quad \text{or} \quad D_o = 20{\cdot}723 + 2{\cdot}204\,I \ \ldots\ldots\text{(ii)},$$

where O stands for the observed outer, and I for the observed inner diameter.

The probable error in determining the value of the inner diameter from that of the outer by equation (i) is given by the expression $\pm {\cdot}6745\,\sigma_1\sqrt{1-r^2}$. In the present case this expression equals $\pm$ ·804 mikrons.

The probable error in determining the outer diameter from the inner by equation (ii) is 2·120 mikrons. The expression for this probable error is the same as that for equation (i) except that σ_2 is written instead of σ_1.

2. *Correlation between outer diameter and colour.*

The methods used in measuring and classifying the colour of *Arcella* shells have been fully described in another section. It will be recalled that the shells were divided into four colour classes, designated *A*, *B*, *C*, and *D*. Class *A* includes the shells lightest in colour and *D* those darkest.

In Table VII. is shown the frequency of the occurrence of the different combinations of colour and size of shells.

TABLE VII.

Correlation between Colour and Outer Diameter in Arcella.

Outer diameter in mikrons.

Colour Class	42—44	44—46	46—48	48—50	50—52	52—54	54—56	56—58	58—60	60—62	62—64	64—66	66—68	68—70	70—72	72—74	74—76	76—78	78—80	80—82	82—84	84—86	86—88	88—90	90—92	92—94	94—96	Totals
A	1	—	—	1	2	6	7	5	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	24
B	—	—	—	2	6	18	33	8	3	—	—	1	—	2	—	—	—	—	—	—	—	—	1	—	—	1	—	75
C	—	1	—	—	4	22	34	9	1	—	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	75
D	—	—	—	2	8	62	82	22	3	1	2	—	1	—	1	2	2	2	4	—	—	1	—	1	—	—	1	197
Totals	1	1	—	5	20	108	156	44	7	1	5	1	3	2	2	2	2	2	4	—	—	1	1	1	—	1	1	371

The colour classes are not quantitatively defined in this table, but they may be considered each as including a definite though unknown portion of the colour scale of some one pigment in the *Arcella* shell. The intensity of this colour may also be considered to increase regularly and gradually from the lower limit of class *A* to the upper limit of class *D*.

The method we have used in obtaining the coefficient of correlation between colour and diameter of shell is that described by Pearson*.

* Pearson, K., *Phil. Trans.*, Vol. 195, A, pp. 1–47.

A fourfold table was formed from Table VII. and is exhibited in Table VIII. The divisions were taken between the outer diameter classes centering at 55 mikrons and 57 mikrons, and between the colour classes *C* and *D*. These seemed on the whole the best divisions to choose. They lie near the medians and satisfy the requirements of making $a+c>b+d$ and of also making $ad>bc$, although they do not make $a+b>c+d$. It is impossible to fulfil this condition without making our horizontal division somewhere within colour class *D*. As a consequence of $c+d$ being greater than $a+b$, k is, of course, negative.

TABLE VIII.

Fourfold Correlation between Colour and Outer Diameter.

Diameter:	Under 56	56 and over	Totals
Colour: Under Class *D*	(*a*) 137	(*b*) 37	(*a*+*b*) 174
Class *D*	(*c*) 154	(*d*) 43	(*c*+*d*) 197
Totals	(*a*+*c*) 291	(*b*+*d*) 80	(*N*) 371

$$h = \cdot 78704,$$
$$k = -\cdot 07778.$$

The equation in r is

$$\cdot 018179\, r^4 - \cdot 063044\, r^3 + \cdot 030608\, r^2 - r + \cdot 012046 = 0.$$

Solving for r by Horner's method, we get

$$r = \cdot 01205.$$

The probable error of this very low coefficient with such a comparatively small number of observations is of course large as compared with the coefficient itself. The value of the probable error in case this r had been computed by the product-moment method would be approximately $\pm \cdot 035$. The value of the probable error for the method here used has not been computed, but it is of course still larger.

Making all due allowance for the size of the probable error it is clearly seen that there is an extremely small degree of correlation between colour and size in the shell of *Arcella* within the limits of size in the series here discussed. It may even be said that practically there is no correlation between these two characters.

To find that there is practically no correlation between darkness of colour and size in *Arcella* shells is an unexpected and rather interesting result, and is apparently contrary to the opinion generally held among zoologists regarding the matter. This result seems to definitely negative any view which would maintain that the *Arcella* shell grows darker with its *cultural* age. Or, to express it in another way, this very low correlation coefficient between colour and size seems to show that we should not expect the $(n+1)$th or $(n+2)$th generation of *Arcella* to be on the average darker in shell colour than the nth. This statement of course assumes what observation clearly warrants, that the shells of the $(n+1)$th and $(n+2)$th generations will be on the average larger than the nth generation shells. It must be repeated, however, that it can only be affirmed that this lack of correlation between colour and size holds for the generations falling within the series of observations here reported. One of the points which impresses one most strongly in following through the history of an *Arcella* culture is that the very minute shells which appear in numbers in the very earliest part of the cultural development are all very light in colour, falling within our colour class *A*. These extremely small individuals are probably developed from spores and form their shells individually entirely *de novo*. The existence of these small, universally light coloured shells early in the course of the development of the culture would indicate that our result of no correlation between colour and size would not hold for the first few generations formed in the culture.

On the further question as to whether the individual shell changes in colour during the course of its existence, we have at present no evidence to offer.

3. *The rate of change of the average size of shell with the age of the culture.*

As has been stated earlier in the paper the measurements extended over a period of approximately three weeks. Between the time when the first and the last measurements were taken there was evidently an opportunity for the average size of the individuals in the culture to change. The culture was in a flourishing condition during this period, and it seemed a matter of some interest to determine how much of an increase in the average size of the individuals occurred.

The cards on which the measurements were recorded were numbered consecutively in the order of measuring, the card bearing the record of the first individual measured being numbered 1, the next 2, and so on up to the last individual. This consecutive numbering furnishes a method of approximating to the desired determination. The cards recording the measurements of the first 500 individuals were arranged in 10 classes of 50 individuals each. The first class contained the first 50 *Arcellae* measured, the next class the second 50 and so on to the tenth class, which contained the last 50 individuals. Then the cards in each class were arranged into arrays with reference to outer diameter. In this way was formed a double-entry table with position in the order of measurement

as the subject character and the outer diameter as the relative character. The mean outer diameter for each of the 10 "age" arrays was then computed. The results are shown in Table IX.

TABLE IX.

Mean Outer Diameters of Arcellae at Successive Stages in the Development of the Culture.

Order of Measurement	Mean Outer Diameter in mikrons
First 50 ...	55·48
Second 50 ...	56·20
Third „ ...	55·56
Fourth „ ...	55·48
Fifth „ ...	55·44
Sixth „ ...	56·20
Seventh „ ...	57·46
Eighth „ ...	55·20
Ninth „ ...	54·52
Tenth „ ...	56·18

It will be seen at once that there is very little definite shift of the mean towards a higher value in the higher "age" classes. The straight line best fitting these means is almost exactly vertical. To get a numerical idea of the amount of the shift, the average of the five means of the first 250 individuals may be compared with the average of the five means of the 250 individuals last measured. The mean diameter for the first 250 individuals measured is 55·632 mikrons; for the last 250 it is 55·912 mikrons. The difference between these values is ·280 mikron, which is evidently a practically insensible difference.

It may be concluded that in a period of time of approximately three weeks the average size of *Arcella* shells in a culture, as estimated by random samples of 50, does not sensibly increase.

IV. Summary.

The present paper comprises the results of a statistical study of variation and correlation in the shell of the common rhizopod, *Arcella vulgaris*.

The points especially investigated were: (i) the variation in the total diameter of the shell, (ii) the variation in the opening of the shell, (iii) the variation in the colour of the shell, (iv) the correlation between the total diameter of the shell and the diameter of the opening, (v) the correlation between the colour and the total diameter of the shell. The frequency distributions and the constants deduced from them, and the correlation tables and coefficients for the various characters are presented.

The results and conclusions may be summarized as follows:

1. Both the diameter of the shell and of the opening show a reasonably high variability. The frequency distributions for both characters are unimodal and markedly skew.

2. The opening in the shell is decidedly more variable in size than is the whole shell, size in both cases being indicated by the respective diameters.

3. The coefficients of variation for the two diameters (opening and total shell) present values in very fair accord with those obtained by Simpson for size characters in *Paramœcium*, showing that these organisms are approximately equally variable in corresponding characters.

4. There is a high degree of positive correlation (coefficient = ·84) between the diameter of the shell and of the opening.

5. Regression and characteristic equations for determining the mean total diameter of the shell associated with a given diameter of the opening and *vice versâ*, are given.

6. There is found to be an extremely small degree of correlation (coefficient = ·01) between the size of the shell and its colour within the size limits of the series of individuals discussed. The correlation is so small as to be practically insensible.

7. There is no sensible change in the average size of the shells as indicated by random samples, within the period of the life of the culture studied. This period covered approximately three weeks in time.

MISCELLANEA.

Craniological Notes.

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Explanatory.

The conclusions drawn by anatomists and anthropologists from examinations of series of crania are at present based upon two types of judgment. The first type of judgment is what we may term the method of appreciation; the anatomist examines the cranial series and by a process of general appreciation classes the series as belonging to a certain race, or throws out certain individuals as belonging to a different race. Sometimes the appreciative inspection will lead the craniologist to classify a series in this way into five or six types or races,—two or three pure types and two or three mixed types. The bases of these appreciative judgments are qualitative, they cannot be criticised by the biometrician, they belong to the *arcana* of the anatomist's training. The biometrician can only place alongside such judgments the results of quantitative investigations, which are deduced by difficult and often very laborious statistical theory. The statistical method in craniology is difficult and laborious because the series dealt with are usually so small that conclusions can only be drawn as the balance of a very fine weighing of probable errors, and accordingly the statistician can frequently only say: "This I think is the balance of probabilities." He is compelled to stand in wonder and admiration before the definite facts which the method of appreciation appears to elicit.

Now qualitative appreciation does not admit of exact statement of the wherefore of the judgment in print; accordingly anatomical craniologists have been in the habit of publishing measurements and dealing with a few statistical arguments based on means or graphical polygons of frequency or even rough tables of correlation. Here the biometrician is at liberty to step in and express a perfectly definite judgment on the statistical processes adopted and the conclusions deduced. In nine cases out of ten he can confidently assert that the anatomical appreciation is only obscured by the statistical arguments used in its favour. The data are either insufficient for any statistical conclusion whatever; or they are unaccompanied by any determination of their probable errors on which alone a judgment could often be based; or the very *principia* of the theory of statistics are clearly unknown to the handlers of the data. It is idle to deny the obvious fact that the numerical arguments used by such authorities as

Virchow, His, Topinard, Broca, Davis, Flower, and a multitude of others, are hopelessly inadequate to maintain the structure reared on them. No valid arguments at all as to race or type can be based on such statistics, and the biometrician can assert this without in the least criticising the appreciative judgment of these great anatomical authorities.

The object of the present series of *Craniological Notes* is to bring home to craniologists the need for the revision of their statistical methods. They will therefore deal principally with recent craniological work, and if they criticise it occasionally with vigour, it will be with the sharpness of the surgeon's knife, which is handled in the real interests of the patient. Our criticism will not be purely negative, but reconstructive.

I. *Professor Aurel von Török's attack on the Arithmetical Mean.*

By Karl Pearson, F.R.S.

A very voluminous craniological memoir has recently been issued by Professor Aurel v. Török assisted by Herr Gabriel v. László. It is entitled:

Ueber das gegenseitige Verhalten der kleinsten und grössten Stirnbreite so wie der kleinsten und grössten Hirnschädelbreite bei Variationen der menschlichen Schädelform. "Zeitschrift für Morphologie und Anthropologie," Band IV. S. 500—88.

This memoir consists of two parts, first a vigorous criticism of the use of the arithmetic mean in craniology, and secondly an investigation of the correlation which exists between certain cranial breadths. The data with which the authors deal are very ample, consisting of 2000 skulls "aus älteren und jüngeren Friedhöfen Ungarns." Presumably the crania were adult and of one sex. This first note deals only with Professor v. Török's attack on the use of the arithmetic mean.

Professor v. Török's attack is of the following character. He says that under the expression "type" can only be understood what is characteristic of the totality of any class of things, something which enables us at once to distinguish them from other things:

"So kann...die Bestimmung eines Typus in gar nichts anderem bestehen, als dass man unter dem Mehrerlei der Einzelmerkmale dasjenige herausgreift, was in der grossen Ueberzahl anzutreffen ist. Dies ist doch einfach und klar. Nun muss die Frage gestellt werden: kann durch eine arithmetische Mittelzahl das Charakteristische, d. h. das in der grossen Ueberzahl Vorkommende ausgedrückt werden? Dies wäre nur unter der einzigen Bedingung möglich, wenn auf die Werthgrösse der arithmetischen Mittelzahl die überwiegende Mehrheit der Einzelfälle fallen würde. Entweder, oder. Nun soll man eine solche arithmetische Mittelzahl, welche die überwiegende Mehrheit der Einzelfälle in sich vereinigt, doch endlich einmal auch aufzeigen! Es wurde bisher tausend- und tausendmal der Typus mittels der arithmetischen Mittelzahl schon als bestimmt angegeben, aber es soll noch derjenige Anthropologe ausfindig gemacht werden, der sagen könnte, dass er mit seiner arithmetischen Mittelzahl auch wirklich die Ueberzahl der Einzelfälle zum Ausdruck gebracht hat" (p. 511).

Professor v. Török here clearly considers that the type is something which differentiates an *individual* of one population from an *individual* of a second population. As a matter of fact the arithmetic mean may, but does not always, enable us to distinguish one *race* or population from a second *race* or population. Any such population or race is only *fully* defined by a number of statistical constants, means, modes, variabilities, correlations, etc. and will only be distinguishable from a second race provided its constants one or more or all of them differ by quantities sensibly greater than the probable errors of random sampling from those of the second race. A knowledge of the arithmetic means only would never enable one to say of an individual skull that it belonged to one race and *not* to another. A knowledge of the *variabilities and correlations as well* of these races might enable us to state *the degree of probability* that the skull belonged to one race rather than to the other.

If it is necessary for Professor v. Török at this epoch in the history of craniology to define the "type" as that which is the rule, and to demonstrate against the great body of craniologists that the arithmetic mean does not define the type, this science must indeed be in a parlous condition! One can hardly grasp that this can be the state of affairs in any branch of knowledge, or that its workers have never heard of Quetelet, Galton, or even Stieda!

But Professor v. Török perceives that he cannot leave the matter here. He states that the arithmetical mean according to the doctrine of Gauss is that value of the character which most frequently repeats itself in the population, i.e. it coincides with what biometricians are accustomed to term the *mode*. Our authors, merely taking the rough frequencies of their 2000 skulls, show that in three cases out of four the group which corresponds to the arithmetic mean falls short of other groups of frequency in its neighbourhood, and accordingly argue that the arithmetic mean is idle:

Wie wir sehen, trifft der Fall der häufigsten Wiederholung (Vertretung) der Werthgrösse der arithmetischen Mittelzahl bei den vier Variationsreihen nur ein einziges Mal ein. In der Variationsreihe der grössten Hirnschädelbreite wird sie sogar durch vier andere Einzelwerthe übertroffen. Man frage sich doch angesichts dieser Thatsache, was man Sicheres auf den Beweis einer arithmetischen Mittelzahl behufs unserer Typusforschungen bauen kann? Und wenn man ohne Voreingenommenheit die Sache so wie sie ist beurtheilt, muss man denn nicht zur Einsicht gelangen; dass eben, weil ihre Werthgrösse nie die absolute Mehrheit und auch nicht immer die relative grösste Vertretung aufweist, wir genöthigt sind behufs Aufstellung eines Typus ausser ihr unbedingt noch andere Werthgrössen des betreffenden Maasses in Betracht zu ziehen! (S. 517).

Of course other constants must be dealt with in addition to completely describe a given population. *Only* Professor v. Török's attack fails absolutely, because he has neglected to deal with the variations in his frequency groups due to random sampling, and these as we will show later are such that there is no really *significant* difference between the actual modes,—not his apparent modes (*Scheingipfeln*),—and his means.

Lastly, Professor v. Török says that the position of the arithmetical mean in the whole group of variation must be considered.

Wie schon der Ausdruck "Mittelzahl" andeutet, erweckt der Begriff einer solcher Zahl in uns die Vorstellung, dass ihre Werthgrösse in der Mitte der betreffenden Variationsreihe (Zahlreihe) steht. Thut sie aber dies? Wenn dies der Fall wäre, so böte sie uns innerhalb der so vielen Veränderlichkeiten unserer kraniometrischen Zahlreihen wenigstens einen fixen Punkt, wo man das Problem einer Typusbestimmung anheben könnte (S. 517).

In other words, to use the biometric term, Professor v. Török questions whether the mean gives the median. By the simple process of taking the characters of his first and last groups of variants adding and halving them, Professor v. Török shows that the arithmetic mean does not give the median! There is not the least attempt to obtain a scientifically accurate median, nor to ascertain whether the difference between that and the mean is a sensible difference or not. The writer has clearly not the most elementary conception of the theory of statistics, nor even a merely physical appreciation of the effects of random sampling, nor again of differences due to different methods of grouping. The whole problem of graduating raw data is a sealed book to him! Yet here are his final conclusions,—sweeping for craniology, revolutionary, indeed, for all science!

Auch nach den hier vorgetragenen Thatsachen, muss ein jeder selbständig denkender Forscher die Verfehlheit aus der arithmetischen Mittelzahl, einen Typus herausspeculiren zu wollen, doch einsehen.... Es erwächst nun eine unabweisliche Pflicht, und zwar in erster Reihe für die tonangebenden Autoritäten der heutigen Anthropologie: entweder, wenn möglich, ihr bisheriges Verfahren klar und einwurfsfrei zu rechtfertigen; oder, wenn dies ihnen nicht gelingt, mit gutem Beispiel voranzugehen und die Typusfrage von diesem alten Irrthume endlich einmal zu befreien. Ein weiteres Stillschweigen ist gewiss nicht mehr motivirt, die Angelegenheit muss doch einmal geschlichtet werden. Der Kampf um die Wahrheit ist das einzig berechtigte *punctum saliens* fur wissenschaftliche Discussionen, neben welchem alle übrigen persönlichen Rücksichten verstummen müssen! (S. 520).

Let us now see exactly in what Professor v. Török's criticism consists. It contains three separate charges against the arithmetic mean:

(i) It does not give the rule, something characteristic of every member of a group termed by craniologists the type.

Obviously and clearly it cannot, and if any craniologist thinks it does, he should begin his studies *ab initio* with a reading of Quetelet's works.

(ii) It is not identical with the *mode*.

(iii) It is not identical with the *median*.

These defects (i), (ii), and (iii) make the mean of no service at all in craniological discussions.

Now let us consider (ii) and (iii) in the light of Professor v. Török's own data treated by an adequate statistical theory. Table I. gives his data for greatest forehead breadth (S. 509) and for greatest skull breadth (S. 509). I selected these two series out of the four given because they looked in Professor v. Török's diagrams the "skewest," and therefore, if there was a sensible distinction between mean, mode and median, I thought it would certainly be evidenced in these.

TABLE I.

Greatest Forehead Breadth				Greatest Skull Breadth			
mm.	Frequency	mm.	Frequency	mm.	Frequency	mm.	Frequency
100	1	*123*	122	*120*	1	*145*	128
101	0	*124*	109	*121*	0	*146*	118
102	0	*125*	80	*122*	0	*147*	115
103	4	*126*	81	*123*	0	*148*	84
104	5	*127*	60	*124*	1	*149*	78
105	5	*128*	45	*125*	0	*150*	52
106	3	*129*	46	*126*	0	*151*	46
107	14	*130*	33	*127*	6	*152*	29
108	13	*131*	26	*128*	1	*153*	30
109	21	*132*	17	*129*	3	*154*	23
110	33	*133*	19	*130*	13	*155*	19
111	50	*134*	4	*131*	20	*156*	8
112	43	*135*	7	*132*	28	*157*	5
113	49	*136*	1	*133*	36	*158*	3
114	89	*137*	2	*134*	36	*159*	5
115	99	*138*	0	*135*	58	*160*	4
116	108	*139*	1	*136*	60	*161*	0
117	124	*140*	0	*137*	88	*162*	1
118	114	*141*	0	*138*	108	*163*	1
119	151	*142*	0	*139*	118	*164*	0
120	148	*143*	1	*140*	119	*165*	0
121	141	*144*	0	*141*	143	*166*	0
122	130	*145*	1	*142*	138	*167*	0
				143	127	*168*	0
				144	140	*169*	1

Now these series are so nearly symmetrical that it seemed sufficient to graduate them with a curve of the type: $y=y_0\left(1+\frac{x}{a}\right)^p e^{-\gamma x}$, where $p=\gamma a$: see *Phil. Trans.* A., Vol. 186, p. 367.

We find :

Greatest Forehead Breadth.	*Greatest Skull Breadth.*
Mean = 120·0475 mm.	Mean = 142·7095 mm.
S.D. = 5·8124 mm.	S.D. = 5·8374
μ_2 = 33·783,910	μ_2 = 34·075,776
μ_3 = 11·370,311	μ_3 = 17·810,678
p = 1192·0125	p = 497·9270
y = 5·9425	y = 3·8264
a = 200·5918	a = 130·1279
y_0 = 137·273	y_0 = 136·684
Mode = 119·8792 mm.	Mode = 142·4482 mm.

The mode being the origin the equations to the frequency distributions are respectively :

$$y = 137{\cdot}273\left(1+\frac{x}{200{\cdot}5918}\right)^{1192{\cdot}0125} e^{-5{\cdot}9425x},$$

and :

$$y = 136{\cdot}684\left(1+\frac{x}{130{\cdot}1279}\right)^{497{\cdot}9270} e^{-3{\cdot}8264x}.$$

The high values of p and a show how very close the distributions are to the Gaussian curve in which mean, mode, and median coincide. Let us consider this matter a little more at length by finding the probable errors of μ_3 and d, the distance between mean and mode. The values of these probable errors are to be found in the paper on the *Probable Errors of Frequency Constants**, and we thus find for :

Greatest Skull Breadth.	*Greatest Forehead Breadth.*
$\mu_3 = 11{\cdot}3703 \pm 17{\cdot}3500$	$\mu_3 = 17{\cdot}8107 \pm 7{\cdot}5783$
d = ·1683 ± ·1081	d = ·2163 ± ·1088.

Thus μ_3 is in one case slightly more than double the probable error and may, perhaps, be significant. In both cases d is less than twice its probable error and is therefore very likely to be insignificant. Actually this is the slender sort of basis upon which Professor von Török would discard the arithmetic mean from craniology! Looking at the result a little more closely, we see that Professor v. Török having no conception of the probable error of any sub-group of frequency places his mode at the *Scheingipfel* of 121 mm. for the forehead breadth. The actual mode of the graduated observations is at 119·88 mm., only ·17 mm. from the mean at 120·05 mm. ; and the difference between the two is really within the limits of the errors of random sampling. Turning to the maximum skull breadth, the actual mode is at 142·45 mm. and the mean at 142·71 mm., while Professor v. Török points with triumph to *Scheingipfeln* at 141 and 144 as if they subverted the whole theory of the arithmetic mean! Again we see that the true mode as obtained from a proper system of graduation is quite close to the mean, i.e. within a small fraction of a millimetre, and the difference is quite possibly due to the errors of random sampling.

In order to illustrate these points still further the normal curves for the two series were calculated; they are :

Greatest Forehead Breadth.	*Greatest Skull Breadth.*
$y = 137{\cdot}273\, e^{-\frac{1}{2}\left(\frac{x}{5{\cdot}8124}\right)^2}$	$y = 136{\cdot}684\, e^{-\frac{1}{2}\left(\frac{x}{5{\cdot}8374}\right)^2}$.
Origin at mean: 120·0475 mm.	*Origin at mean:* 142·7095 mm.

* *Biometrika*, Vol. II. p. 273. See also *Phil. Trans.* A., Vol. 191, p. 275.

Table II. gives the observed and calculated values. Applying the method for testing goodness of fit given in *Biometrika*, Vol. I. p. 155, we find in the first case: $\chi^2 = 40{\cdot}429$ and $P = {\cdot}37$, and in the second case, $\chi^2 = 33{\cdot}362$ and $P = {\cdot}69$. Or, supposing the Hungarian data dealt with by Professor v. Török to actually follow the normal or Gaussian curve, in every three samples of 2000 skulls he would on the average have found one fitting theory worse for forehead breadth than his sample actually does; and for skull breadth every two out of three samples of 2000 skulls would on the average give a worse result. In the face of such probabilities as this any sound statistician would not hesitate to say that for skull breadths Professor v. Török's Hungarian data obey the normal law of frequency, exactly as we have proved is the case for many series of other cranial measurements. The accompanying *diagrams* show the observations fitted with the theoretical curves and demonstrate at a glance how idle is any argument based on *Scheingipfeln*.

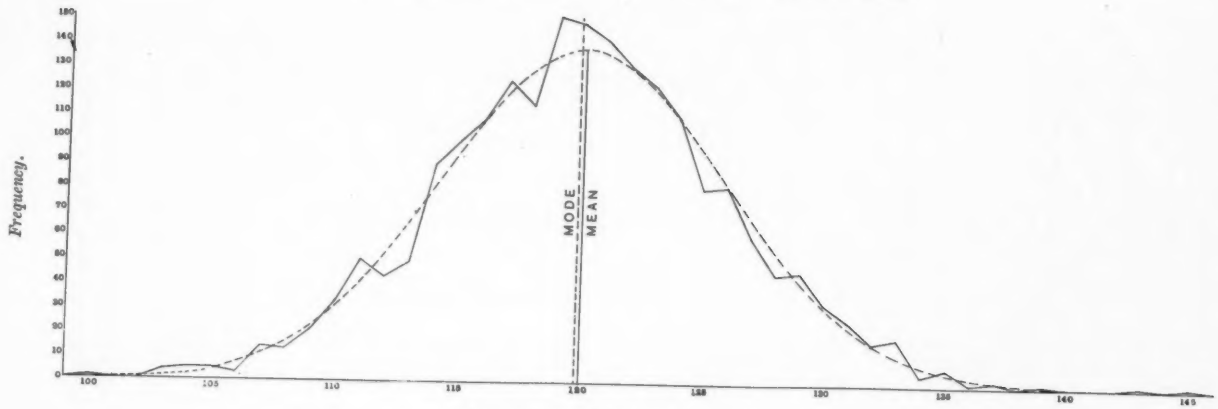
TABLE II.

mm.	Greatest Forehead Breadth					mm.	Greatest Skull Breadth				
	Frequency		mm.	Frequency			Frequency		mm.	Frequency	
	Observed	Calculated		Observed	Calculated		Observed	Calculated		Observed	Calculated
Below *103*	1	2·5	*125*	80	95·5	Below *127*	2	5·5	*148*	84	90·6
103	4	1·9	*126*	81	81·2	*127*	6	3·7	*149*	78	76·5
104	5	3·1	*127*	60	67·2	*128*	1	5·8	*150*	52	62·7
105	5	4·8	*128*	45	53·9	*129*	9	8·7	*151*	46	49·9
106	3	7·4	*129*	46	42·0	*130*	13	12·9	*152*	29	38·6
107	14	11·1	*130*	33	31·8	*131*	20	18·3	*153*	30	29·0
108	13	16·0	*131*	26	23·3	*132*	28	25·5	*154*	23	21·1
109	21	22·7	*132*	17	16·6	*133*	36	34·3	*155*	19	15·0
110	33	30·9	*133*	19	11·5	*134*	36	45·0	*156*	8	10·3
111	50	40·9	*134*	4	7·8	*135*	58	57·2	*157*	5	6·6
112	43	52·7	*135*	7	5·1	*136*	60	70·6	*158*	3	4·7
113	49	65·8	*136*	1	3·2	*137*	88	84·7	*159*	5	2·8
114	89	79·9	*137*	2	2·0	*138*	108	98·7	*160*	4	1·7
115	99	94·2	*138*	0	1·2	*139*	118	111·6	*161*	0	1·1
116	108	107·7	*139*	1	0·7	*140*	119	122·6	*162*	1	0·6
117	124	119·5	above			*141*	143	130·8	*163*	1	0·3
118	114	128·9	*139*	2	0·8	*142*	138	135·5	above		
119	151	134·9				*143*	127	136·0	*163*	1	0·4
120	148	137·1				*144*	140	133·5			
121	141	135·2				*145*	128	126·4			
122	130	129·6				*146*	118	116·5			
123	122	120·6				*147*	115	104·3			
124	109	108·8									

Had the mean differed from the mode, modern statistical theory could have deduced the modal value without appealing to *Scheingipfeln*. As it turns out, however, for these skulls' breadths Gaussian theory is perfectly applicable: *mean, mode and median sensibly coincide*, and Professor v. Török's attack on the arithmetical mean fails absolutely, and this because he is attempting, as so many other craniologists do, to advance without any knowledge of statistical theory.

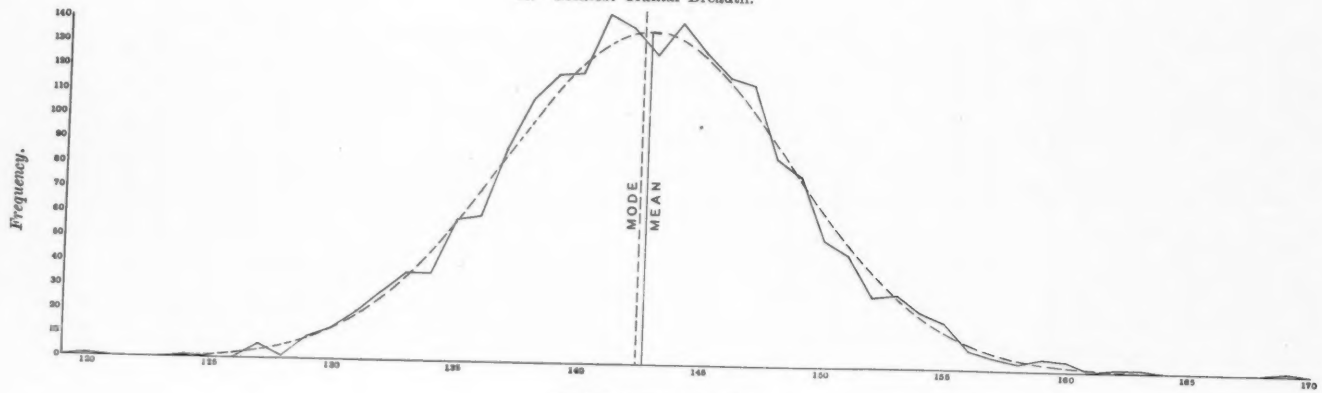
If the median were to coincide with the mean Professor v. Török tells us that there would be a fixed point to start the "Problem einer Typusbestimmung" from. Well, it actually does

2000 ♂ Hungarian Skulls. I. Greatest Forehead Breadth.



Greatest Forehead Breadth.

II. Greatest Cranial Breadth.



Greatest Cranial Breadth.

coincide in Professor v. Török's data within the errors of random samplings. The arithmetic mean can be freed from the charges he brings against it. Can he solve the "Problem einer Typusbestimmung" on these lines? Personally I think not. "Der Kampf um die Wahrheit" in the craniology has for its solely legitimate *punctum saliens* the recognition that craniology is a branch of biometry, and can only be followed profitably when the modern theory of statistics has been properly studied.

II. *Homogeneity and Heterogeneity in Collections of Crania.*

By Karl Pearson, F.R.S.

In a review* by Mr C. S. Myers of a memoir by Miss C. D. Fawcett†, one of the biometric workers at University College, London, exception is taken to the arguments adduced in favour of the homogeneity of the Naqada prehistoric crania. There are many statements in Mr Myers' review which it would be easy to traverse, but as the writer expresses himself as in sympathy with what he is pleased to term the "new path," a consideration of one of them will suffice to show to what extent he appears to be fit at present to enter upon it.

The statement is as follows:

> The question, moreover, arises, are we entitled to consider either the Naqada or the above English skulls as belonging to people of a single race? The authors think that we are "justified in treating our material as homogeneous and in speaking of a Naqada *race* and not merely of the Naqada crania" (p. 424). "If the [Naqada] material were markedly heterogeneous the variability in length and breadth of skull ought to be large as compared with admittedly homogeneous material" (p. 424). The standard deviations of the male Naqada skulls and of Bavarian, Aino, French, and English male series as regards skull-length are 5·722, 6·088, 5·936, 7·202, 6·446 respectively, and as regards skull-breadth are 4·612, 5·849, 3·897, 6·068, 4·976 respectively. These deviations (and the "coefficients of variability" derived therefrom) are considered by the authors to be small enough to warrant the conclusion that the Naqada crania, the old Bavarian crania of Professor Ranke, and the Whitechapel English crania of Professor Thane constitute each a homogeneous series. They have left neglected the question whether a much larger standard deviation would result, were we to consider a series, say, of forty-nine male skulls of most diverse ethnic types, composed, *e.g.*, of fifteen Australians, seven Guanches, fifteen Eskimos, and twelve Chinese. This is the material which the reviewer set himself to work out, taking the data haphazard from Flower's well-known catalogue of skulls in the Royal College of Surgeons' Museum. The results gave him a standard deviation of 8·389 for the skull-length, and of 7·002 for the skull-breadth. We see, then, how small is the difference of variation between the Naqada skulls of Professor Pearson's series (which are of a "homogeneous character") and a series which is as heterogeneous as it could well be. Are we, then, not justified in considering the Naqada skulls and the others of Professor Pearson's series as if they had sprung from a mixture of races? If not, at least the problem is less simple than the writers appear to think.

The mean of the variabilities of the skull lengths given in the above paragraph is 6·2788 and of the skull breadths is 5·0804. Mr Myers mixing Australians, Guanches, Eskimos and Chinese finds a variability of skull length = 8·389 and of skull breadth = 7·002. He then points to the differences (2·1102 and 1·9216) and triumphantly asks how such small differences can be of any importance! But had Mr Myers had a mathematical training he would know that nothing is "small" absolutely, but only relatively to something else, and had he had a statistical training he would have known that he must compare it with the variability of these variabilities i.e. the standard deviation of the standard deviations of the skull measurements. Now the standard deviation of the above series of skull length variabilities = ·5185 and that of the

* *Man*, February, 1903, p. 13.

† *Biometrika*, Vol. I. pp. 408—467.

skull breadth variabilities is ·7996. The first "small" difference is therefore 4·07 times its standard deviation, the second is 2·40 times its standard deviation. In other words whatever sort of group the Naqada, Bavarian, Aino, French, and English male cranial series make, the odds are 42,552 to 1 against such an excess of variability as Mr Myers found for his mixed series of skull lengths belonging to a number of that series, and 121 to 1 against such an excess as he found for the skull breadths occurring in such a series! It is such odds as these the combination of which can hardly fall short of 4,000,000 to 1 and which no sane man in practical conduct could disregard, that amount to "small" differences from the standpoint of the old school of craniologists! But the whole matter deserves further consideration from a wider standpoint. What fairly homogeneous data have we for variability of skull length and breadth? In the first place the list above contains the variability of 860 French male skulls from the Paris catacombs; I have dealt with this series in previous papers and expressed doubts as to its homogeneity, I have published too other cases of variability for much more homogeneous French series,—Parisians* and French peasants. The first of these is the larger of the two series, and though both have much less variability than the catacomb skulls I take the Parisians as the better series. We have then the following series, to which I have added three cases of measurements on the living head:

Series.	*Length.*	*Breadth.*	*Number.*
Ainos	5·936	3·897	76
Bavarians	6·088	5·849	100
Parisians	5·942	5·214	77
Naqadas	5·722	4·612	139
English†	6·085	4·976	136
Cambridge Undergraduates	6·161	5·055	1000
English Criminals	6·046	5·014	3000
Oraons of Chota Nagpur	5·916	4·397	100

In this series of eight the Naqada crania stand easily first for least variability in length, and third in the order of least variability for breadth.

Now it is impossible to regard these data, which cover, so far as I am aware, practically all the available data for variation in skull or head lengths hitherto worked out, without seeing (i) that variation in head length is practically the same as variation in skull length, and (ii) that both for very different cranial series are extremely nearly six. This corresponds with the coefficient of variation about three, which I have used in this case for many years. Anything that differs much from six—like the Parisian catacomb series—I should *à priori* suspect of heterogeneity. Now if we take the above series we find for the mean variability of head length 5·987 and of head breadth 4·877, and for the standard deviations of these variabilities ·1292 and ·5454 respectively. In this case the deviations of Mr Myers' heterogeneous series are 2·402 and 2·125, or respectively 18·6 and 3·90 times their standard deviations. In other words, the odds against such a highly variable series being of the same character as those we have given above are 6×10^{76} to 1 and 20,832 to 1 respectively! The correlation between length and breadth variations as given by the above data is $-$ ·0197 or *negative*. The combined odds are therefore greater than if the events were independent. In other words the odds against Mr Myers' mixture belonging to the class of cranial series we have grouped together above as homogeneous are more than:

$$12 \times 10^{80} \text{ to } 1 !$$

* Data provided for me by the courtesy of M. Manouvrier. The other crania were brought to the catacombs from grave-yards which had been in use for several centuries.

† Using the results for the glabella maximum length, for which I have to thank Dr W. R. Macdonell, who is at work on these crania. The value cited by Mr Myers is the horizontal length, all that was available for Miss Fawcett's purpose at the time of her memoir.

Mr Myers asks in the face of these odds, the immensity of which is beyond my powers of realisation, "Are we not justified in considering the Naqada skulls and the others of Professor Pearson's series as if they had sprung from a mixture of races?"

There is only one reply to Mr Myers—these or any other series may originally have sprung from a mixture of races, but they possess something which differentiates them *totally* from his mixture of Australians, Guanches, Eskimos, and Chinese, something which the trained biometrician, who realises what is relatively "large" and what is relatively "small," can almost see on inspection. Mr Myers has been, I understand, lecturing on the "new anthropometry." It seems very like the old, and about it we can only cite Mr Myers' own words: "Never again, it is to be hoped, will the old [? new] school be tolerated which collects a few measurements, dissects them, and publishes ill-founded conclusions."

As to the general principles to be deduced from the above figures I think they are these. The heterogeneity of any series the variability of which for skull length exceeds 6·5, or for skull breadth exceeds about the same quantity, should be suspected and the series subjected to close examination. If the variability of the skull length be less than 5·5, or of the skull breadth less than 3·3, then we must suspect that the series is a rather stringently selected sample. This rule will generally enable us to distinguish between heterogeneity due to a mixture of crania from diverse races, and the homogeneity of a single race, which may indeed be the product of a number of generations of cross-breeding such as we may assert of modern English, French or Germans, but hardly with the same certainty of Ainos or Bengal castes.

III. *Preliminary Note on Interracial Characters and their Correlation in Man.*

By S. Jacob, A. Lee, D.Sc., and Karl Pearson, F.R.S.

(1) A distinction has been drawn in this Journal* between *intraracial* and *interracial* correlation, and the present preliminary note is intended to emphasise the importance of this distinction. If we take a race of which we have sufficient data and determine its type† by a number of characteristics, either by forming the means or the modes for the frequency-distributions of these characteristics in the race, we shall find that within the race an individual who diverges from the type of the race for one character will probably do so for a second, and that there is for the total of individuals within the race an interrelationship between these divergences—expressible by their coefficient of correlation. This correlation within the race is an *intraracial* coefficient, it predicts only the probable within the race itself, and must be very cautiously extended from one race to a second without *à priori* justification. The coefficient of correlation thus determined varies as a rule from race to race. Because the correlation between length and height of head of Aino ♂s is ·5, it does not follow that this Aino characteristic may be applied to prehistoric Egyptians or modern Germans. In fact, whereas within these races a long-headed Egyptian or Aino was probably a high-headed individual also, a long-headed German tends to be low-headed. It is accordingly very misleading to predict from observations within one race what are the probable relationships between characters in a second; still less legitimate is it to predict from the coefficient of correlation in one race what would be the probable value of a defective measurement in an individual of a second race‡. Our knowledge at present tends to

* Vol. I. pp. 460 and 461.

† 'Type' is here defined as what distinguishes one population from a second, and not any member of the first from any member of the second.

‡ An illustration of this may be given from a recent paper by Professor A. v. Török and G. V. László (*Zeitschrift für Morphologie und Anthropologie*, Bd. IV. pp. 500—588). The authors had

show that correlation varies from race to race, and that only for certain special organs (related in a particular way to the manner in which selection has differentiated the two races from a common stock) will the regression coefficients on which prediction depends remain the same for the two races. Only by an extensive tabulation of the differences between regression coefficients shall we be able ultimately to predict the evolution of racial differences, and accordingly there must always be danger in extending intraracial results from one race to a second; we are leaping over the very fence we have ourselves erected when we classified them as *separate* races, for the source of that separation is written from the evolutionary side in the very differences of regression coefficients which we disregard when we predict from one race to a second. But it is not only in predicting from one race to an individual of a second that we need caution. How far may we even assert that what holds within one race holds for the races of the world taken as a whole? A long-headed Aino is probably tall-headed; are the long-headed races of the world tall-headed races? A platyrrhine Naqada was chamaeconchic. Is racial platyrrhiny usually associated with racial chamaeconchy? There are many such problems which can only be answered when a much more ample tabulation of racial types than we have at present has been provided. Still there is an obvious and correct method of approaching and solving such problems; we must correlate the type values of the characters for as many races as possible. Such correlation coefficients have been termed interracial coefficients of correlation, and their discovery must form the basis of an exact theory of race for any species, in particular of a theory of race in man. The present note is only preliminary. Its chief function is by an illustration or two to serve as a caution against the extension of intraracial results to interracial conclusions, or against the application of intraracial results to reasoning on individual organisms belonging to different or possibly quite unknown races. We confine our attention for the present to characters of the human head.

(2) *Illustration I.* **Correlation of Breadths on the Living Head.** As material we took the mean values of 57 castes or tribes from Risley's *Tribes and Castes of Bengal*, selecting those which contained the data for 50 to 100 individuals each. In all instances where Risley's means looked suspicious new averages were struck, and several rather serious errors were in some cases found. Six non-suspicious cases taken at random and tested were found to be sensibly in agreement with Risley's results. The three measurements dealt with were the cephalic breadth, the minimum frontal breadth, and maximum bizygomatic breadth. Let us term these B_C, B_F, and B_Z respectively; let M_C, M_F, M_Z be the corresponding means of the racial means and σ_C, σ_F, σ_Z, the standard deviations of the respective racial means. The correlations will be represented by r_{CF}, r_{CZ}, and r_{FZ} for the interracial relations between cephalic breadth and minimum frontal breadth, between cephalic breadth and maximum bizygomatic breadth, and between minimum frontal breadth and maximum bizygomatic breadth respectively.

apparently splendid material, 2000 Hungarian skulls; they deal with four characters, the maximum and minimum skull breadths, and the maximum and minimum forehead breadths, and their object is to deduce the probable value of one of these breadths from one, two, or three of the others. The direct statistical method was to form six correlation tables, and determine the six coefficients; the multiple regression formulae would then have given the most probable value of any character for given values of the other three. The authors, however, deal at very great length with the arrays and subarrays of the frequency surface for the multiple characters, whereas the correct statistical procedure would have given the type and variability of any subarray at once. Had this been done it would have been possible, for example, to have at once predicted from the least forehead breadth and greatest skull breadth the probable greatest forehead breadth of any Hungarian skull. But beyond this we could not venture to go until we had shown that the regression coefficients calculated for Hungarians closely hold for other races. Professor von Török's application of his Hungarian data to an individual skull of a totally different race, the Neanderthal skull, may give a near result or not, but the application is quite unwarranted by our present knowledge and is full of dangers.

Then we find:

$$M_c = 140{\cdot}498, \quad M_F = 102{\cdot}160, \quad M_z = 132{\cdot}216,$$
$$\sigma_c = 4{\cdot}5734, \quad \sigma_F = 3{\cdot}1034, \quad \sigma_z = 3{\cdot}0011,$$
$$r_{FZ} = {\cdot}5694, \quad r_{zc} = {\cdot}6949, \quad r_{cF} = {\cdot}5415.$$

It will be seen that from the interracial standpoint the cephalic breadth is more closely related to the bizygomatic breadth than either of these to the minimum frontal breadth. Thus a reconstruction for a race of the bizygomatic breadth would be better made from the cephalic than from the frontal breadth. There can be no doubt that we have in Bengal a very great mixture of races, though it may be open to doubt whether it is sufficiently wide to admit of our supposing the above correlation coefficients to be close enough to be true interracial values. In particular a maximum breadth of the living head of 140·5 could hardly correspond to a maximum skull breadth of more than 130 to 132 mm. But such a skull breadth would be extremely small for European races, where, for example, we have: Bavarians 150·5, Whitechapel English 140·0, French 145·2, and Hungarians 142·7. The above values must therefore be looked upon as merely provisional and suggestive.

Now let us compare these values with those within a single tribe. Take first the Oraon tribe of Chota Nagpur. We have:

$$M_c = 139{\cdot}31, \quad M_F = 101{\cdot}97, \quad M_z = 130{\cdot}46,$$
$$\sigma_c = 4{\cdot}5093, \quad \sigma_F = 3{\cdot}2166, \quad \sigma_z = 3{\cdot}8273,$$
$$r_{FZ} = {\cdot}5543, \quad r_{zc} = {\cdot}4093, \quad r_{cF} = {\cdot}5867.$$

Now in the case of skulls the frontal breadth is the character which is usually preserved longer than the bizygomatic or cephalic breadths, we will therefore write down the regression equations for the latter breadths.

Interracial Regression Equations.

(i) $P_z = 75{\cdot}961 + {\cdot}55065\, F.$

(ii) $P_z = 54{\cdot}796 + {\cdot}26421\, F + {\cdot}35892\, C.$

(iii) $P_c = 58{\cdot}969 + {\cdot}79805\, F.$

(iv) $P_c = -7{\cdot}249 + {\cdot}31802\, F + {\cdot}87174\, Z.$

Here P_z and P_c are the probable bizygomatic and cephalic breadths of a race as deduced from their known mean frontal breadths, or the combination of these and their cephalic or bizygomatic breadths respectively. Applying these equations to predict the mean bizygomatic and frontal breadths of the Oraon tribe we have:

From (i) $P_z = 132{\cdot}1$, observed 130·5,
(ii) $P_z = 131{\cdot}7$, „ 130·5,
(iii) $P_c = 140{\cdot}4$, „ 139·3,
(iv) $P_c = 138{\cdot}9$, „ 139·3.

We see at once that the mean bizygomatic and cephalic breadths of the tribe are given fairly closely by the interracial regression formulae. But how would these formulae apply to widely different data? Not having measurements on the living head available, let us take cranial measurements, allowing 8 mm. for the flesh on all three breadths. This is probably too much for the frontal breadth and possibly too little for the cephalic breadth, but it will serve our purposes of testing the formulae.

We have the following data for males:

	Naqada	*Bavarians*	*Aino*
M_C	134·87	150·47	141·20,
M_F	91·06	103·70	96·20,
M_Z	125·63	135·00	137·30.

Applying our formulae these give:

TABLE I.

Formulae used	Naqada		Bavarians		Aino	
	Calculated	Observed	Calculated	Observed	Calculated	Observed
P_z from (i)	122·5	125·6	129·5	135·0	125·3	137·3
„ (ii)	124·2	125·6	133·2	135·0	127·9	137·3
P_C from (iii)	130·0	134·9	140·1	150·5	134·1	141·2
„ (iv)	132·7	134·9	144·9	150·5	144·5	141·2

Now it is clear that these results fall very wide of the mark—giving with one exception values mostly far too small; or we conclude that: *No satisfactory interracial formulae by which either zygomatic or cephalic breadths could be deduced from frontal breadth can be obtained even from data as varied as that provided by the tribes and castes of Bengal.*

While an interracial formula based on that data gives fairly good results for a special tribe it cannot be applied to such diverse material as the Naqada, Bavarian, and Aino series. In fact our Bengal material has throughout a remarkably small cephalic breadth as compared with the frontal and zygomatic breadths, and we get formulae practically of no service at all for such crania as the German or Aino. We have taken too limited a group of human races. To obtain interracial formulae we must clearly proceed on a much wider basis, and such an investigation we hope to undertake at a later date.

In the next place we turn to an individual race and write down the equations by which the probable cephalic (p_c) and bizygomatic (p_z) breadths might be predicted for an individual head of this race.

For the statistical constants of the Oraon tribe given above we have:

$$p_z = 63{\cdot}21 + {\cdot}65954\,F,$$
$$p_c = 55{\cdot}45 + {\cdot}82245\,F.$$

For a second race we take 52 ♂ Naqada skulls for which the three breadths C, F, and Z are known. We find:

$$M_C = 133{\cdot}68, \quad M_F = 90{\cdot}52, \quad M_Z = 125{\cdot}39,$$
$$\sigma_C = 4{\cdot}3596, \quad \sigma_F = 4{\cdot}4364, \quad \sigma_Z = 5{\cdot}4914,$$
$$r_{FZ} = {\cdot}5695, \quad r_{ZC} = {\cdot}0440, \quad r_{CF} = {\cdot}1107.$$

The corresponding formulae for reconstructing the bizygomatic and cephalic breadths from the minimum frontal breadth are:

$$p_z = 61{\cdot}58 + {\cdot}70497\,F,$$
$$p_c = 123{\cdot}84 + {\cdot}10875\,F.$$

The marked feature of the Naqada results is the great drop in the correlations between the cephalic and zygomatic and between the cephalic and the frontal breadths when we pass from

the living head results to cranial measurements. Is this something peculiar to the Naqada race or to cranial as distinct from living head measurements? To test this result the cranial constants were worked out for the cases of the English (Whitechapel) skulls* and for the Theban mummies†.

English Crania.

$M_C = 140{\cdot}70$, $M_F = 98{\cdot}01$, $M_Z = 130{\cdot}05$,
$\sigma_C = 5{\cdot}2781$, $\sigma_F = 4{\cdot}0577$, $\sigma_Z = 5{\cdot}4651$,
$r_{FZ} = {\cdot}6238$, $r_{ZC} = {\cdot}4768$, $r_{CF} = {\cdot}4075$.

Theban Mummies.

$M_C = 136{\cdot}76$, $M_F = 93{\cdot}82$, $M_Z = 128{\cdot}32$,
$\sigma_C = 4{\cdot}45$, $\sigma_F = 4{\cdot}31$, $\sigma_Z = 5{\cdot}22$,
$r_{FZ} = {\cdot}342$, $r_{ZC} = {\cdot}250$, $r_{CF} = {\cdot}298$.

Thus we see that while the English crania have high correlations between the breadths, of the same general order as those determined for the living head, yet the Theban mummies give much lower results approaching far nearer to the Naqada low correlations. The fact that the Theban mummies still differ considerably from the closely allied Naqada race is consonant with, indeed confirmatory of, the view expressed by Fawcett and Lee‡ that in the 4000 years which intervened between the two groups, the differentiation that had gone on was especially in the cranial breadths.

In all the intraracial results whether for skull or living head the correlation between zygomatic and cephalic breadths is less than that between zygomatic and frontal breadths—a result sensibly different from that obtained from the interracial Bengal data, where the correlation between zygomatic and cephalic breadths is very sensibly the largest. For the English crania we have the reconstruction formulae:

$$p_Z = 47{\cdot}71 + {\cdot}84016\,F,$$
$$p_C = 88{\cdot}75 + {\cdot}53006\,F.$$

For the Theban crania:

$$p_Z = 89{\cdot}46 + {\cdot}41410\,F,$$
$$p_C = 107{\cdot}90 + {\cdot}30768\,F.$$

Clearly the regression formulae differ immensely as we pass from Naqada to Theban and Theban to English series. Hence also the predictions will vary, and conclusions drawn from one race cannot be extended to a second.

Again it is quite true that we must expect a difference between constants obtained on the living head and on the skull, but we know by experience that certain variations and correlations can be fairly close in the two cases for the same or closely allied races. We see in this case indeed that the correlations and regression coefficients for bizygomatic on minimum frontal breadth are not very widely divergent for Oraon and Naqada, but the correlations between maximum cephalic breadth and the maximum bizygomatic or the minimum frontal breadth are of a totally different order as we pass from the Indian to the Egyptian race. To emphasise this let us take five individual Oraons and five Naqadas§ and predict from their frontal breadths

* The full measurements on these skulls have now been completed by Dr W. R. Macdonell, and we hope they will shortly be published.

† Data given in the *Anthropologische Sammlungen Deutschlands*, E. Schmidt, "Leipziger Privatsammlung." The constants for these skulls are given provisionally as they have not been revised.

‡ *Biometrika*, Vol. I. pp. 432—3.

§ They were taken absolutely at random, i.e. the 10th, 20th, 30th..... individuals on the list.

their cephalic and bizygomatic breadths. Using again 8 mm. for difference of living head and skull breadths we have the following Table:

TABLE II.

Observed Frontal Breadth	Bizygomatic Breadth			Cephalic Breadth		
	Oraon Formula	Observed	Naqada Formula	Oraon Formula	Observed	Naqada Formula
1st Oraon 103	131	132	137	140	131	142
2nd Oraon 99	128·5	130	134	137	137	142
3rd Oraon 107	134	138	139	143	141	143
4th Oraon 102	130·5	128	136	139	152	142
5th Oraon 103	131	121	137	140	137	142
1st Naqada 90·6	120	123·5	126	129	123·5	134
2nd Naqada 102·0	128	130·0	133·5	138	133·0	135
3rd Naqada 90·5	120	124·0	125	128·5	132·5	134
4th Naqada 92·5	121·5	123·5	127	130	135·0	134
5th Naqada 96·5	124	124·0	130	133	135·5	134

From these results we deduce:

	Oraon Formula	*Naqada Formula*
Bizygomatic Breadth:		
Mean Error of 5 Oraon	3·8	6·8
„ „ 5 Naqada	2·3	3·3
Cephalic Breadth:		
Mean Error of 5 Oraon	5·2	6·6
„ „ 5 Naqada	4·4	3·3

It is clear that

(i) The formulae give by no means very close results when we predict the bizygomatic and cephalic breadths of an individual from the formula for his own race, and (ii) may give very divergent results if we predict an individual from the formula for a second race. In other words; *A knowledge of the most probable values of the bizygomatic or cephalic breadths reconstructed from the frontal breadth in the case of one race, is not a knowledge of the most probable values in a second unallied race.*

The coefficients of correlation and the standard deviations of these breadths vary widely from race to race, and accordingly the simple or multiple regression formulae will also vary.

For example, the following values are given for the Neanderthal skull by Professor v. Török*:

$$F = 107 \text{ mm.}, \quad C = 147 \text{ mm.}$$

The cephalic maximum breadth predicted from the minimum frontal breadth would be 144 from the English formula, 143 from the interracial Bengal formula, 142 if predicted from the Oraon tribe, 141 from the Theban formula, and 140 if predicted from the Naqada crania.

* *loc. cit.* p. 584.

For the *Pithecanthropus* (Dubois) we have

$$F=87 \text{ mm.}, \quad C=133 \text{ mm.},$$

and the reconstructed values of C from F are from the interracial Bengal formula 127, if predicted from the Oraon tribe 126, 135 if predicted from either the English or Theban formula, and if predicted from the Naqada crania 133.

Clearly the accuracy of such predictions varies immensely with the race used in making the prediction. It is not safe to lay very much stress on the prediction of an individual from its own racial formula; it is quite unsafe to judge what will happen in an individual case from the correlation constants of a second and very diverse race. Professor v. Török, without graduating his data—as is actually done in the multiple regression formulae—but by simply arguing on the modes of subarrays of multiple correlation series, has drawn conclusions and comparisons as to skulls of other races*. Until he has shown constancy of regression coefficients for the given breadths for all races of man, any argument from one race to a second is quite invalid. The results already proven and those about to be given show how dangerous is the reasoning by which intraracial results are extended from one race to a second, or by which intraracial and interracial results are interchanged the one with the other.

(3) *Illustration II.* **Correlation of Cephalic and Nasal Indices.** We have dealt with this for two sets of living races in the male. Taking the same series of 57 tribes and castes of Bengal we find:

$$M_{CI}=75{\cdot}804, \quad M_{NI}=81{\cdot}282,$$
$$\sigma_{CI}=2{\cdot}9195, \quad \sigma_{NI}=6{\cdot}2556,$$
$$r_{CN}=-{\cdot}20160.$$

Taking 51 races from an appendix to Denniker's recent work on the races of man, Dr Alice Lee found†:

$$M_{CI}=77{\cdot}961, \quad M_{NI}=75{\cdot}949,$$
$$\sigma_{CI}=3{\cdot}8231, \quad \sigma_{NI}=11{\cdot}0081,$$
$$r_{CN}=-{\cdot}32639.$$

We have accordingly the following reconstruction formulae, where i denotes a probable, I an observed index:

Living Head from Bengal Data.

Cephalic Index from Nasal Index: $i_C=83{\cdot}452-{\cdot}09409\,I_N$,
Nasal Index from Cephalic Index: $i_N=114{\cdot}027-{\cdot}43197\,I_C$.

* *loc. cit.* pp. 584–8. Professor v. Török tries to predict from the minimum forehead and maximum cephalic breadths of the Neanderthal skull its maximum forehead breadth, using the ungraduated sub-arrays of the Hungarian correlation data. His process is fallacious (*a*) from the standpoint of the theory of probability, for he ought to have graduated his material by calculating the multiple regression coefficients, and (*b*) from the fact that he extends intraracial conclusions for modern Hungarians to a very different race—that of the Neanderthal man. It would be a most valuable bit of craniological work to deduce the accurate correlations for Hungarian crania from Professor v. Török's material.

† These results give a scientific classification of cephalic index and nasal index. Half the races lie above, half below 78, say. Hence 78 should be the boundary between brachycephaly and dolichocephaly in *living* races. A quarter of the variations are below 75·38 and a quarter above 80·54. Hence indices of 75·5 and 80·5, say, should be taken as the boundaries of hyperdolichocephaly and hyperbrachycephaly. Similarly for the nasal index in *living* races we have the divisions: Below 68·5 hyperleptorrhiny, from 68·5 to 76 leptorrhiny, from 76 to 83·5 platyrrhiny, above 83·5 hyperplatyrrhiny.

The Bengal results are for less wide racial ranges and we do not think it desirable to classify the living head indices on their basis. The systematic classification of races will be dealt with at length later when more ample data have been worked out.

Living Head from Denniker's Data.

Cephalic Index from Nasal Index: $i_c = 86{\cdot}570 - {\cdot}11335\, I_N$,

Nasal Index from Cephalic Index: $i_N = 149{\cdot}216 - {\cdot}93980\, I_c$.

Now these results are extremely interesting. We see that platyrrhine characters are interracially associated with dolichocephally and *vice versâ* in quite a marked degree. We have in each case a quite sensible negative correlation.

The first thing then we are tempted to ask is: whether this is true intraracially? We know already that it is true for the Naqada crania*. The following give the results for two Bengal races for the living head.

Murmi Tribe, Chittagong Hills.	*Oraon Tribe of Chota Nagpur.*
$M_{CI} = 79{\cdot}914$, $M_{NI} = 74{\cdot}889$,	$M_{CI} = 75{\cdot}481$, $M_{NI} = 86{\cdot}250$,
$\sigma_{CI} = 3{\cdot}3250$, $\sigma_{NI} = 6{\cdot}0248$,	$\sigma_{CI} = 3{\cdot}3632$, $\sigma_{NI} = 7{\cdot}7830$,
$r_{CN} = -{\cdot}2284$,	$r_{CN} = -{\cdot}2392$.

The reconstruction equations from these races are:

Murmi Tribe: $i_c = 89{\cdot}353 - {\cdot}12604\, I_N$,

$i_N = 112{\cdot}983 - {\cdot}41383\, I_c$,

Oraon Tribe: $i_c = 84{\cdot}396 - {\cdot}10336\, I_N$,

$i_N = 128{\cdot}030 - {\cdot}55352\, I_c$.

Now these intraracial results are of the same kind as the interracial results, and, considering the smallness of the data dealt with, not widely different in numerical magnitude. We may, we think, conclude accordingly that the association of platyrrhine and dolichocephalic characters is intraracial as well as interracial and the degree of this association has much the same quantitative magnitude in both cases†. It seems legitimate in this instance to draw general conclusions from intraracial to interracial results as far as the living head is concerned.

(4) *Illustration III.* **On the Interracial Relationships of the Orbital to the Cephalic and Nasal Indices of the Cranium in Man** (♂).

Denniker gives for a few races from data of very diverse worth the mean orbital, cephalic and nasal indices. The results obtained by Dr Alice Lee are as follows:

Orbital and Cephalic Index.	*Cephalic and Nasal Index.*	*Nasal and Orbital Index.*
(21 cases)	(16 cases)	(30 cases)
$M_{OI} = 85{\cdot}786$, $M_{CI} = 75{\cdot}367$,	$M_{CI} = 74{\cdot}000$, $M_{NI} = 52{\cdot}231$,	$M_{NI} = 50{\cdot}287$, $M_{OI} = 87{\cdot}023$,
$\sigma_{OI} = 2{\cdot}9172$, $\sigma_{CI} = 4{\cdot}0895$,	$\sigma_{CI} = 3{\cdot}4595$, $\sigma_{NI} = 4{\cdot}1210$,	$\sigma_{NI} = 4{\cdot}4205$, $\sigma_{OI} = 9{\cdot}8969$,
$r_{OC} = {\cdot}4486 \pm {\cdot}1176$.	$r_{CN} = -{\cdot}4460 \pm {\cdot}1354$.	$r_{NO} = -{\cdot}1088 \pm {\cdot}1217$.

* *Biometrika*, Vol. I. p. 455. The reconstruction formulae in this case are:

$$i'_c = 78{\cdot}054 - {\cdot}09914\, I_N,$$

$$i_N = 67{\cdot}206 - {\cdot}22094\, I_c,$$

equations which naturally differ totally from those for the living head and which are at once seen to be absolutely inapplicable to individual German or Aino crania.

† For example for nasal index $= 100$: Bengal data give cephalic index $= 74$, Denniker's data $= 75$; for nasal index $= 50$: Bengal data give cephalic index $= 79$, and Denniker's data $= 81$. The results are less in agreement if the nasal index be predicted from the cephalic.

The paucity of races dealt with, and the heterogeneity of measurers and of series used, make these results of very small value, and they are only given here tentatively, while larger series of more numerous races are being reduced. But even thus some probable conclusions can be more or less definitely stated, i.e.

(*a*) The general statement that platyrrhine races are dolichocephalic is confirmed by cranial measurements.

Considering the probable error of the correlation of the cranial cephalic and nasal indices, that correlation does not differ very widely from that on the living head obtained from Denniker's data. What do differ widely are the mean and *especially the variability* of the nasal indices for races when measured on the living head and on the skull. It may well be questioned how far this variability is not peculiar to the personal equation of the observer and is therefore not a true anthropological character.

(*b*) There is quite a sensible correlation between orbital and cephalic indices, and it is positive. Or: the brachycephalic races tend to round orbits, and the dolichocephalic races to elongated orbits. This as far as the Naqada crania are concerned has been shown to be an intraracial as well as an interracial association.

(*c*) There is some evidence to show that platyrrhine races have elongated orbits.

The correlation between orbital index and nasal index is negative, but it is not definitely sensible compared with its probable error in the small series at present available. This agrees with the intraracial conclusion drawn from the Naqada crania.

(5) *Illustration IV.* **On the Interracial Relationship between the Length and Breadth of the Living Head.**

Hitherto although interracial correlations have been shown to differ from intraracial values, we have only dealt with cases in which these correlations were of the same sign, and the reader might be induced to draw the temptingly fascinating conclusion that interracial and intraracial correlations are always qualitatively alike. In order to convince the reader that no conclusion of this kind is allowable we propose to deal in this last illustration with the length and breadth correlations.

Taking our fifty cases from Risley's *Bengal Tribes* we find for maximum length and breadth of living head the interracial results:

$$M_L = 184{\cdot}64, \quad M_B = 140{\cdot}00,$$
$$\sigma_L = 2{\cdot}2368, \quad \sigma_B = 4{\cdot}6005,$$
$$r_{LB} = -{\cdot}2917.$$

Thus we see that a "principle of compensation" applies. A long-headed race is likely to be a narrow-headed race, and a broad-headed race a short-headed race. This conclusion is essentially interracial, and not intraracial. Intraracially we find that the correlation of length and breadth of living head or of skull while varying remarkably is *positive*. Thus it is so, for English (heads and skulls), French, German, Aino, Naqada and other cranial series*.

Or, again take the Oraon tribe of Chota Nagpur, we find:

$$M_L = 184{\cdot}61, \quad M_B = 139{\cdot}31,$$
$$\sigma_L = 5{\cdot}9160, \quad \sigma_B = 4{\cdot}3970,$$
$$r_{LB} = {\cdot}0655.$$

Thus the correlation is small and positive,—far from the very sensible negative interracial value.

* See *Biometrika*, Vol. I. p. 457.

Hence we see that the "principle of compensation" which certain anatomists seem to have drawn from the observation of heads in the dissecting room appears to be quite fallacious. The long-headed individual within the race is likely also to be relatively broad, i.e. individuals within the race tend to have generally big or generally small heads. The "principle of compensation" only applies when we compare the mean lengths and breadths of different races. Here the long-headed race is a narrow-headed race and *vice versâ*. This is a curious illustration of how by a false or superficial investigation an erroneous result may be reached,—a result which on an entirely different plane can be justified by a correct theory.

We hope later to publish far more complete intraracial coefficients for the case of man, and lay to some extent the foundation of what we believe to be a scientific theory of race in man. In this preliminary note we are confessedly only touching the fringe of an immense and difficult subject, but we believe that we have indicated the proper method of approaching it.

INHERITANCE OF FINGER PRINTS.

Mr Francis Galton is at work on the inheritance of patterns seen in finger prints, and he would be very glad of aid from any readers of *Biometrika* who will be kind enough to take prints of family groups for him. Applications for the loan of a set of apparatus with schedules and forms for writing and printing should be made to Mr Galton at 42, Rutland Gate, London, S.W., with the letters "F. P." (meaning finger prints) boldly written on the upper left-hand corner of the communication.